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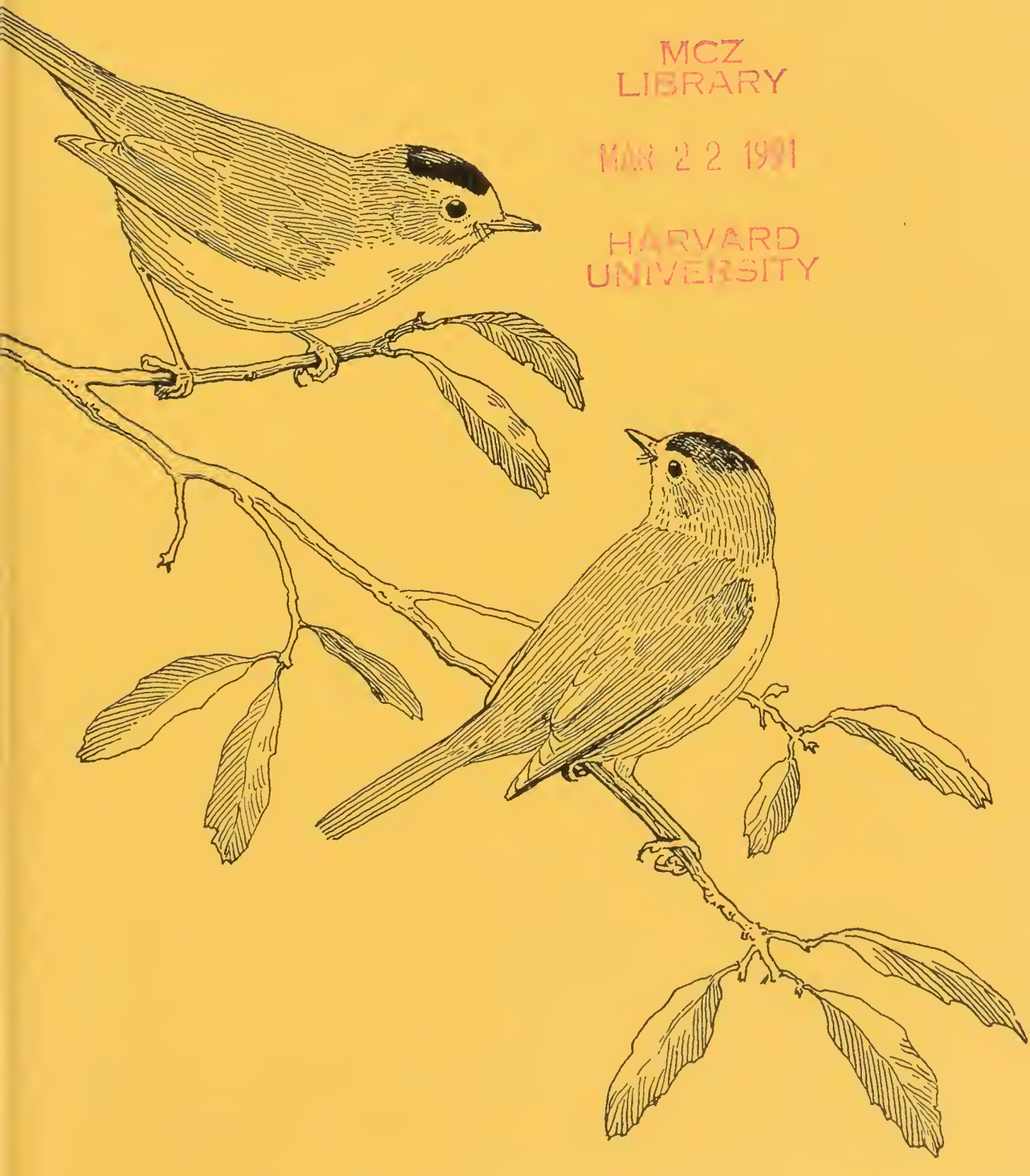

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MORPHOMETRIC ANALYSES OF INTRODUCED AND ANCESTRAL POPULATIONS OF THE EURASIAN TREE SPARROW

VINCENT L. ST.LOUIS[1] AND JON C. BARLOW[1,2]

ABSTRACT.—Birds introduced into new environments by humans provide opportunity to assess microevolutionary change in morphology. The skeletal morphologies of introduced North American and ancestral German populations of the Eurasian Tree Sparrow (*Passer montanus*) were compared to assess: (1) the extent of morphometric differentiation between the introduced and ancestral populations, and (2) whether the introduced populations, which exhibited a decrease in genetic variability relative to the German population, display any such differences in morphometric variability. Sexual dimorphism in certain skeletal characters in *P. montanus* is interpreted to be a result of intraspecific interactions among males and adverse climatic conditions on both sexes. The smaller body size of North American *P. montanus* is thought to result either from interspecific interactions and/or flight habits different from their ancestral counterparts. Significant differences in bill morphology are found between German and North American *P. montanus,* which we believe reflect differences in diet. The North American population shows no significant decrease in intrinsic morphometric variation corresponding to the decrease in genetic variation demonstrated in comparison to German birds. *Received 13 Feb. 1990, accepted 13 April 1990.*

A few founding individuals may yield geographically isolated populations. Often little historical documentation of these founding events exists. As a result, details essential to studies of any morphometric and genetic differentiation between ancestral and introduced populations, e.g., time of separation (and hence time populations have had to diverge), may be lacking. Therefore, well-documented anthropogenic introductions of exotic species, e.g., the introduction of the Eurasian Tree Sparrow (*Passer montanus*) in North America, are important to the evaluation of microevolutionary processes. *P. montanus* was established in North America

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in 1870 when a bird dealer released 12 pairs of West German origin in Lafayette Park, St. Louis, Missouri (Lever 1987). After an early episode of population increase at St. Louis (Merrill 1876), the species began to spread slowly northward in neighboring Illinois. Numbers are now thought to exceed 150,000 in an area of ca 45,000 km^2 (St.Louis and Barlow 1987, 1988).

Comparisons of skin (Barlow 1973) and skeletal (Barlow 1980, Thompson 1983) characters between North American and German specimens showed that Illinois *P. montanus* were smaller than their European counterparts in certain skull and wing-pectoral girdle characters. Size differences between introduced and ancestral populations were attributed to ecological differences between the two areas (Barlow 1973, 1980). Recently we showed that North American *P. montanus* were less variable genetically than the ancestral German birds (St.Louis and Barlow 1988).

Genetic variation within introduced populations is often low following a founding event of a small number of individuals. As a result, introduced populations provide unique opportunities to test two predictions concerning the extent to which genetic variation governs variation in morphometric structure. Mayr (1954, 1963) predicted that low genetic variation should result in decreased morphometric variation. Contrary to Mayr, Lerner (1954) believed that heterozygosity leads to phenotypic stability (heterosis) and that populations with reduced genetic variation should show greater morphometric variation.

Morphometric variation in *P. montanus* was initially examined by Barlow (1980). He found that interpopulation variability (measured by coefficient of variation) was generally homogeneous across sexes and populations, with no evidence (except in wing length) of decreased variability in the North American population. Later, we found no statistically significant morphometric-genetic relationships among six populations of *P. montanus* when comparing: (1) morphometric 'size' with heterozygosity, and (2) estimated degrees of population differentiation using morphometric and genetic distance measures (St.Louis and Barlow 1987). At that time we did not, however, examine the intrinsic variation in morphometric characters of the North American and German birds needed to test the predictions of Mayr (1954, 1963) and Lerner (1954).

In the present study we replicate the earlier studies of Barlow (1980) and Thompson (1983), in an attempt to establish the extent of any further morphometric divergence between the introduced and ancestral populations of *P. montanus*. We also assess intrinsic morphometric variability, in terms of Mayr's or Lerner's predictions, in the North American birds already shown to have decreased genetic variability in comparison to German *P. montanus* (St.Louis and Barlow 1988).

TABLE 1

THE LOCALITIES AT WHICH *PASSER MONTANUS* WERE OBTAINED, COLLECTION DATES, AND SAMPLE SIZES

Location	Latitude, longitude	Collection date (month/ year)	Sample sizes		
			Total	AM[a]	AF[b]
Karlshrule, West Germany	49.00N, 144.58E	11/84	30	8	10
Woodson, Illinois	39.40N, 90.35W	12/83	24	5	7
Naples, Illinois	39.45N, 90.35W	12/83	17	4	5
White Hall, Illinois	39.27N, 90.22W	01/85	52	24	15

[a] Adult males.
[b] Adult females.

METHODS

Specimen acquisition and preparation are detailed in St.Louis and Barlow (1987, 1988). North American populations were obtained between 1983 and 1985 from three sites in Illinois approximately 40–50 km apart (Woodson, Morgan County; Naples, Scott County; and White Hall, Greene County) (Table 1). Specimens representing the ancestral population were obtained in West Germany in 1985 from the region sampled by Barlow (1980) (Table 1). Acquisition of material was limited by permit restrictions.

Morphometric differentiation.—The 16 skeletal measurements previously used by Barlow (1980) and Thompson (1983) were taken only on the adult (skull completely ossified) *P. montanus* using dial calipers accurate to 0.05 mm (see St.Louis and Barlow 1987). Data from Illinois localities were pooled to minimize heterogeneity of variances resulting from the small sample sizes, and in turn tested for homogeneity of variances between the sexes and populations using the F_{max}-test (Sokal and Rohlf 1981) before using parametric statistical tests.

We tested for differences in skeletal features between the sexes in both the North American and German populations with one-way analyses of variance (ANOVA), performed using the SAS package of programs for personal computers (SAS Institute Inc. 1988). Differences between the German and North American populations for each sex were also assessed with ANOVA. However, the probability of incorrectly rejecting one or more true null hypotheses was high because of the large number of ANOVA tests done (16 skeletal characters for each hypothesis) (Rice 1989). Therefore, P values were adjusted to an overall $\alpha = 0.05$ level using the sequential Bonferroni method described by Rice (1989).

Morphometric and genetic variation.—Differences in 'intrinsic' or 'relative' variances for each mensural variable were compared for males and females between the German and North American populations in the manner of Lewontin (1966). Log_{10} transformed variables were used to give a measure of intrinsic variability, and in a multivariate extension of the Levene test (Van Valen 1978), following Fleischer et al. (1983) and Handford (1980), to test the hypothesis that the relative variances were equal between populations. Variables were $\log_{10}$ transformed to generate variances independent of their means (Sokal and Rohlf 1981). Differences in Levene values between the populations were examined by ANOVA.

Individual genotypes, obtained from 39 structural gene loci resolved by starch gel electrophoresis, were analyzed for allelic variation (St.Louis and Barlow 1988). There were no differences in allelic frequencies between age classes or the sexes for each locality; therefore, all specimens from a locality were pooled (St.Louis and Barlow 1988).

TABLE 2

MEAN (MM) AND STANDARD ERRORS OF SKELETAL MORPHOMETRIC CHARACTERS, AND RESULTS FROM ANOVA BETWEEN THE SEXES IN GERMAN (A) AND NORTH AMERICAN (B) POPULATIONS AND BETWEEN NORTH AMERICAN AND GERMAN FEMALE (C) AND MALE (D) POPULATIONS OF *PASSER MONTANUS*

	Germany				North America	
	Females		Males		Females	
Character	N	Mean ± SE	N	Mean ± SE	N	Mean ± SE
Premaxilla length	8	5.72 ± 0.09	10	5.81 ± 0.08	27	5.45 ± 0.05
Narial width	8	0.91 ± 0.02	10	0.92 ± 0.01	27	0.89 ± 0.01
Skull width	8	14.64 ± 0.12	10	14.86 ± 0.08	27	14.63 ± 0.06
Skull length	8	27.09 ± 0.19	10	27.32 ± 0.20	27	26.57 ± 0.11
Dentary length	8	5.13 ± 0.07	10	5.16 ± 0.06	27	4.84 ± 0.05
Mandible length	8	18.58 ± 0.18	10	18.59 ± 0.18	27	18.05 ± 0.07
Coracoid length	8	17.36 ± 0.15	10	17.92 ± 0.18	27	17.17 ± 0.09
Sternum length	8	20.58 ± 0.20	10	21.90 ± 0.22	27	20.76 ± 0.15
Keel length	8	19.26 ± 0.29	10	21.18 ± 0.31	27	19.27 ± 0.18
Sternum depth	8	9.93 ± 0.12	10	10.15 ± 0.11	27	9.41 ± 0.07
Humerus length	8	16.84 ± 0.19	10	17.37 ± 0.14	27	16.75 ± 0.09
Ulna length	7	18.47 ± 0.17	9	19.27 ± 0.15	27	18.17 ± 0.13
Femur length	8	16.56 ± 0.02	10	16.74 ± 0.11	27	16.68 ± 0.08
Femur width	8	1.19 ± 0.02	10	1.19 ± 0.01	27	1.16 ± 0.01
Tibiotarsus length	8	26.13 ± 0.28	10	26.49 ± 0.20	23	26.09 ± 0.15
Tarsometatarsus length	8	17.14 ± 0.15	10	17.50 ± 0.13	26	17.18 ± 0.13

* Significantly different when P values were adjusted to an overall $\alpha = 0.05$ level using the sequential Bonferroni method (Rice 1989).

Wilcoxon's paired signed rank test (Sokal and Rohlf 1981) was employed to measure differences in genetic variation between the German and North American populations. Heterozygosity (direct count) and number of alleles per locus served as measures of genetic variation. Heterozygosity for each locus and number of alleles for each locus were paired for the above testing.

RESULTS

Morphometric differentiation.—Results of the F_{max}-tests showed no significant heterogeneity of variances between the sexes for any skeletal variable in the German or North American populations at the $P \leq 0.05$ level. In male and female samples, only femur width showed a significant heterogeneity of variances between populations for the skeletal variables ($F = 3.17$, df = 7, 26, $P = 0.03$). The significant heterogeneity of variances seen here for only femur width could be attributed to a Type I error (rejection of true null hypothesis). We therefore proceeded with parametric statistical analyses.

ANOVA showed several skeletal measurements in the German and

TABLE 2
CONTINUED

North America Males		A		B		C		D	
N	Mean ± SE	*F*	*P* > *F*	*F*	*P* > *F*	*F*	*P* > *F*	*F*	*P* > *F*
33	5.57 ± 0.04	0.59	0.453	3.21	0.079	6.13	0.019	8.88	0.005
33	0.87 ± 0.01	0.10	0.761	3.30	0.074	0.44	0.514	6.29	0.016
33	14.69 ± 0.05	2.47	0.136	0.58	0.449	0.00	0.962	2.96	0.093
33	26.73 ± 0.07	0.71	0.412	1.54	0.220	5.19	0.029	12.11	0.001*
32	4.98 ± 0.05	0.09	0.762	3.79	0.056	10.22	0.003*	3.43	0.072
32	18.16 ± 0.07	0.00	0.967	1.03	0.314	10.88	0.002*	6.97	0.012
33	17.52 ± 0.08	5.46	0.033	8.40	0.005	1.18	0.285	5.10	0.029
33	21.14 ± 0.12	18.27	0.001*	3.86	0.054	0.38	0.543	9.43	0.004*
33	19.92 ± 0.14	19.83	0.000*	8.19	0.006	0.00	0.982	16.49	0.000*
33	9.73 ± 0.05	1.84	0.194	14.60	0.000*	12.65	0.001*	15.35	0.000*
33	17.00 ± 0.08	5.69	0.030	4.51	0.038	0.21	0.648	5.30	0.027
33	18.56 ± 0.10	12.22	0.004*	6.24	0.015	1.33	0.257	12.01	0.001*
33	16.71 ± 0.07	0.88	0.361	0.13	0.721	0.46	0.504	0.05	0.823
33	1.16 ± 0.01	0.02	0.888	0.14	0.711	3.40	0.074	4.11	0.049
32	26.02 ± 0.14	1.18	0.294	0.31	0.578	0.02	0.890	1.10	0.300
33	17.27 ± 0.11	3.33	0.087	0.32	0.572	0.03	0.855	1.18	0.285

North American populations to be significantly larger in males than in females when *P* values were adjusted using the sequential Bonferroni method (Table 2). Two body core (sternum and keel length) and one wing (ulna length) characters were significantly different between the sexes in German birds. Sternal depth only, however, was significantly different between the sexes in North American birds. As a consequence, the sexes were treated separately in all remaining analyses.

Three and five of the 16 characters in females and males, respectively, were significantly smaller in the North American population when *P* values were again adjusted using the sequential Bonferroni method (Table 2). Two skull (dentary and mandible length) and one body core (sternum depth) characters were smaller in North American females, whereas one skull (skull length), three body core (sternum and keel length, and sternum depth), and one wing (ulna length) characters were smaller in North American males.

Morphometric and genetic variation.—Using the method of Lewontin (1966), only skull length in males and femur width in females showed a

TABLE 3

VARIANCE OF LOG-TRANSFORMED SKELETAL CHARACTERS AND RESULTS OF SIGNIFICANCE TESTS OF LEWONTIN (1966) USED TO DETERMINE DIFFERENCES IN INTRINSIC VARIATION BETWEEN NORTH AMERICAN AND GERMAN FEMALE SKELETAL CHARACTERS IN *PASSER MONTANUS*

Character	Germany N	Germany $s^2\log_{10}x$ ($\times 10^{-4}$)	North America N	North America $s^2\log_{10}x$ ($\times 10^{-4}$)	$\frac{s^2 \text{ (larger)}}{s^2 \text{ (smaller)}}$	df	$F_{0.05}$
Premaxilla length	8	3.26	27	5.19	1.59	26, 7	3.40
Narial width	8	9.31	27	9.03	1.03	7, 26	2.39
Skull width	8	1.02	27	0.79	1.29	7, 26	2.39
Skull length	8	0.71	27	0.86	1.21	26, 7	3.40
Dentary length	8	3.12	27	4.41	1.41	26, 7	3.40
Mandible length	8	1.46	27	0.74	1.97	7, 26	2.39
Coracoid length	8	1.10	27	1.24	1.13	26, 7	3.40
Sternum length	8	1.40	27	2.72	1.94	26, 7	3.40
Keel length	8	3.26	27	4.41	1.35	26, 7	3.40
Sternum depth	8	2.36	27	2.80	1.19	26, 7	3.40
Humerus length	8	1.93	27	1.43	1.35	7, 26	2.39
Ulna length	7	1.09	27	2.49	2.28	26, 6	2.83
Femur length	8	1.51	27	1.10	1.37	7, 26	2.39
Femur width	8	5.99	27	1.86	3.22*	7, 26	2.39
Tibiotarsus length	8	1.69	23	1.36	1.25	7, 22	2.46
Tarsometatarsus length	8	1.22	26	2.58	2.11	25, 7	3.41

* $P \leq 0.05$.

significant decrease ($P \leq 0.05$) in intrinsic variation in the North American *P. montanus* in comparison with German birds. Variation in all other characters in both populations was highly similar (Tables 3 and 4). An ANOVA on Levene variables demonstrated equal variation between the populations for both male ($F = 1.46$, df = 1, 41, $P = 0.23$) and female ($F = 0.32$, df = 1, 33, $P = 0.57$) specimens.

Mean heterozygosity was 0.079 (SE = 0.025, N = 93) in North American specimens and 0.093 (SE = 0.026, N = 30) in German specimens. Mean number of alleles per locus was 1.4 (SE = 0.1) in the North American specimens and 1.5 (SE = 0.1) in the German specimens. For these two measures of genetic variation, Wilcoxon's paired signed rank test indicated a significant difference between the German and North American populations only for mean number of alleles per locus ($T_s = 4$, $P = 0.05$).

DISCUSSION

Morphometric differentiation.—When assessing morphology of a species which exhibits sexual dimorphism, each sex must be analyzed sep-

TABLE 4

VARIANCE OF LOG-TRANSFORMED SKELETAL CHARACTERS AND RESULTS OF SIGNIFICANCE TESTS OF LEWONTIN (1966) USED TO DETERMINE DIFFERENCES IN INTRINSIC VARIATION BETWEEN NORTH AMERICAN AND GERMAN MALE SKELETAL CHARACTERS IN *PASSER MONTANUS*

Character	Germany		North America		$\frac{s^2 \text{ (larger)}}{s^2 \text{ (smaller)}}$	df	$F_{0.05}$
	N	$s^2 \log_{10} x$ ($\times 10^{-4}$)	N	$s^2 \log_{10} x$ ($\times 10^{-4}$)			
Premaxilla length	10	3.71	33	3.11	1.92	9, 32	2.19
Narial width	10	4.52	33	9.92	2.19	32, 9	2.85
Skull width	10	0.52	33	0.67	1.28	32, 9	2.85
Skull length	10	1.03	33	0.45	2.29*	9, 32	2.19
Dentary length	10	2.82	32	6.76	2.39	31, 9	2.86
Mandible length	10	1.73	32	1.00	1.73	9, 32	2.20
Coracoid length	10	1.81	33	1.44	1.26	9, 32	2.19
Sternum length	10	1.97	33	1.92	1.03	9, 32	2.19
Keel length	10	3.99	33	3.19	1.25	9, 32	2.19
Sternum depth	10	2.06	33	1.60	1.29	9, 32	2.19
Humerus length	10	1.11	33	1.41	1.27	32, 9	2.85
Ulna length	9	1.07	33	1.80	1.68	32, 8	3.07
Femur length	10	7.90	33	1.00	1.27	32, 9	2.85
Femur width	10	1.86	33	3.34	1.80	32, 9	2.85
Tibiotarsus length	10	1.03	32	1.72	1.67	31, 9	2.86
Tarsometatarsus length	10	1.09	33	2.54	2.33	32, 9	2.85

* $P \leq 0.05$.

arately when: (1) differences in morphology at the interpopulation level are examined, and (2) forces which may have led to the differentiation between the populations are investigated (Price 1984). Determining how the two sexes in any population respond to environmental parameters in effect assesses the cause and perpetuation of dimorphism of secondary characteristics (Price 1984).

Three sternal and wing characters were significantly smaller in females than in males in the German population, whereas only sternum depth was significantly different between the sexes in the North American population. Differences in size between the sexes in the closely related House Sparrow (*Passer domesticus*) are thought to reflect selection favouring large males in male to male interactions (sexual selection) (e.g., Johnston and Selander 1971, Johnston 1973, Johnston and Fleischer 1981) but may be modified by differential selection of body size classes of males and females during adverse climatic conditions (e.g., Johnston 1969, Johnston et al. 1972, Fleischer and Johnston 1982; also see McGillivray and John-

ston 1987). For example, the larger dominant males within a population are also at a selective advantage with respect to thermoregulation (small surface area to volume ratio) during severe winter storms (Johnston and Selander 1973), whereas large subadult females are probably selected against (McGillivray and Johnston 1987).

Bill size is believed to be correlated with food size and other aspects of foraging (e.g., Hespenheide 1973; Abbott et al. 1975, 1977; Schluter and Grant 1984). We detected, however, no sexual size dimorphism in bill characters in North American *P. montanus contra* Thompson (1983), or in the German birds. Thompson (1983) thought that bill dimorphism was related to the influence of environmental parameters affecting females only (mean July temperature [e.g., Johnston 1969]) and possibly because of a broader spectrum of food resources in North America relative to Germany. Because bill size of males and females is similar in both the North American and German populations of *P. montanus,* we assume that the sexes have not diverged in resource use (i.e., exploitation of different niches).

Head- and bill-related characters, however, differed significantly for both males and females between North American and German birds. The differences found here between certain North American and German head- and bill-related characters in males were not found by Barlow (1980) or Thompson (1983), suggesting that the foraging-related differences noted herein were not previously recognized. In winter in North America, *P. montanus* was seen feeding virtually 100% of the time on cereal grains (corn, wheat, soybeans, and livestock feed) (pers. obs.). This diet differs from that of *P. montanus* in Germany where winter food consisted of 79% seeds of weeds, 9.6% cereal (oats, barley, wheat), 8.4% vegetal parts, and 3% glumes and plant fibers (Keil 1973). In summer, North American *P. montanus* fed on different arthropod prey than did European *P. montanus* (Anderson 1973, 1984).

Foraging-related differences between North American and German *P. montanus* may be attributed further to interactions between *P. montanus* and *P. domesticus.* The population size increase and aggressiveness of North American *P. domesticus* may have contributed to the slow rate of population growth of *P. montanus* (Summers-Smith 1988). Anderson (1973) demonstrated a syntopic relationship between *P. montanus* and *P. domesticus* in North America which differs from the interactions of the two species in most of Eurasia (Summers-Smith 1988, Lack 1971, Dyer et al. 1977, Anderson 1984). Winter diet and foraging sites for both *Passer* species resembled each other closely in North America, where both species often feed together in large mixed flocks (Anderson 1973, pers. obs.). In West Germany, however, winter foraging sites differed between

P. montanus and *P. domesticus* (Keil 1973). The relative size of winter food items of the two species is unknown. *Passer montanus* summer diet overlapped with that of *P. domesticus* to a greater extent in North America than in Europe (Anderson 1984). Anderson (1980), however, documented a similarity in summer food size in North America between *P. domesticus* and *P. montanus,* suggesting that these two species do not separate resources by size. We assume, therefore, that change in bill morphology in *P. montanus* is not related to interspecific interactions with *P. domesticus* on summer diet.

A significant decrease in sternal depth contributed to the degree of size reduction in both male and female North American specimens when compared with German adults. North American males, however, have shown a significant decrease in other sternal- and wing-related characters in comparison with German specimens not seen in females. These differences, previously explained in terms of flight constraints (i.e., migration; Barlow 1980), might also be attributable to interspecific interactions between *P. montanus* and *P. domesticus.* In North America, *P. domesticus* is known to displace *P. montanus* from nest sites (Widmann 1889, pers. obs.). Anderson (1973) demonstrated experimentally in Missouri that the larger *P. domesticus* excluded the smaller *P. montanus* from nest boxes with hole dimensions large enough for both species to enter. Perhaps then some modicum of selection for smaller body size (sternal and wing characters) might be attributable to size of opening of nest cavities, especially in males, because males both choose and initially defend the nest site (Anderson 1973). The decrease in sternal depth of North American females suggests that they have responded in a similar manner in favoring nest cavities with a small entrance.

In the present study, we found no significant differences between North American and German birds for any leg-related characters, *contra* Barlow (1980). Barlow (1980) attributed significantly smaller leg characters in North American *P. montanus* to possible perching-related differences between North American and German birds or character covariation in the inherently smaller North American specimens.

Morphometric and genetic variation.—Although we found only a trend toward decreasing heterozygosity in North American compared with German populations, there was a significant pairwise decrease in mean number of alleles per locus in the North American population. Such a pattern of genetic variation may result from the effects of a bottleneck in population size on the mean number of alleles per locus and heterozygosity in a population (Nei et al. 1975). In general, mean heterozygosity is expected to increase faster in a population than mean number of alleles, the former resulting from effective population size and rate of increase following the

founding event and the latter being a function of the mutational rate (Nei et al. 1975; also see St. Louis and Barlow 1988).

Mayr (1954, 1963) predicted that following a founding event or genetic bottleneck, a reduction in genetic variation would produce a decrease in morphometric variation apparent in the founder population. Lerner (1954), on the other hand, proposed that highly heterozygous individuals have enhanced developmental homeostasis, resulting in a reduction of morphometric variation. We detected no evidence in support of Mayr's (1954, 1963) or Lerner's (1954) predicted relationships. Only skull length in males and femur width in females showed a significant decrease in intrinsic variation in the North American population which might correspond to the observed reduction in allozyme variation. Because these significant differences appear to be isolated cases, it is presumed they are of little genetic significance. These results correspond to those already discussed, in which selection, both natural and sexual, acts on the morphometric characters to produce a mean optimal phenotype. This optimal phenotype most likely has a corresponding standard amount of intrinsic variation about its mean. This standard amount of variation has also been noted for example in introduced North and South American populations of *P. domesticus* as compared with ancestral European populations (Johnston and Klitz 1977), in the Fox Sparrow (*Passerella iliaca*) (Zink et al. 1985), and in the Rufous-collared Sparrow (*Zonotrichia capensis*) (Handford 1980).

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JOINT MEETING OF THE COOPER ORNITHOLOGICAL SOCIETIES

Three special events are tentatively scheduled for the joint meeting of the Cooper and Wilson Ornithological Societies 15–19 May 1991, at Norman Oklahoma: (1) a symposium on the Interface of Science and Conservation in Latin American Ornithology, (2) a symposium on the effects of Forest Fragmentation on Birds, and (3) a workshop on Endangered Passerines.

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EUROPEAN STARLING FIDELITY TO DIURNAL ACTIVITY CENTERS: ROLE OF FORAGING SUBSTRATE QUALITY

DONALD F. CACCAMISE[1]

ABSTRACT.—The information center hypothesis, the most commonly cited explanation for communal roosting behavior, assumes a roost-centered foraging distribution. Nonetheless, European Starlings (*Sturnus vulgaris*), as well as several other communally roosting species, have a foraging distribution centered on a single diurnal activity center (DAC) which is central to the distribution of roosts they use. The "patch-sitting hypothesis" integrates DAC-based foraging behavior into an alternate explanation for communal roosting behavior. One prediction of this hypothesis is that foraging substrate quality should decline on DAC's as increasing proportions of the local roosting population become associated with large roosting congregations, i.e., when more individuals leave their DAC's to forage elsewhere. I examined this prediction by assessing foraging substrate quality on DAC's through measures of feeding success on the most commonly used DAC-based foraging substrate—lawns. My goals were to determine the importance of foraging substrate quality in DAC fidelity and to identify the factors contributing to the decline in use of lawns during late summer. I found a substantial seasonal decline in foraging success, suggesting lower foraging substrate quality on DAC's when (1) use of lawn habitats normally declines, and (2) starlings leave their DAC's to forage and roost at distant sites. These results agree with the prediction that foraging substrate quality declines when starlings leave their DAC's to forage elsewhere, and thereby provide new support for the patch-sitting hypothesis. *Received 19 Sept. 1989, accepted 27 Aug. 1990.*

During the post-breeding roosting season (June–November) European Starlings (*Sturnus vulgaris*) show ardent fidelity to the same small (2–4 km^2) diurnal activity center (DAC) over many weeks, while at night they use a variety of different communal roosts (Caccamise et al. 1983, Morrison and Caccamise 1985). Such DAC-based roosting behavior has been directly observed in Common Grackles (*Quiscalus quiscula,* Morrison and Caccamise 1990), American Robins (*Turdus migratorius,* Bovitz 1991), American Crows (*Corvus brachyhynchos,* Stouffer and Caccamise, unpubl. data), and may be indirectly inferred in Red-winged Blackbirds (*Agelaius phoeniceus,* Johnson 1979), wing-tagged starlings in Great Britain (Feare 1984), Cattle Egrets (*Bubulcus ibis,* Siegfried 1971), and Great Blue Herons (*Ardea herodias,* Krebs 1974).

The information center hypothesis (Ward and Zahavi 1973) is the most commonly cited explanation for communal roosting behavior (Mock et al. 1988). It carries the implicit assumption of a roost-centered foraging distribution. If roosts are the location where individuals "learn" the lo-

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cation of new feeding sites, then the roost should lie at the center of the group of feeding sites used by individual birds. DAC-based species have a foraging distribution that is DAC-centered, with foraging concentrated on a single small area which itself is central to the distribution of the roosts that are used (e.g., Morrison and Caccamise 1985) This is clearly contrary to the roost-centered assumption of the information exchange hypothesis. Violation of the roost-centered assumption casts serious doubt on the importance of information transfer (sensu strictu, Ward and Zahavi 1973) as the primary cause for the formation of roosting assemblages in any DAC-based roosting species.

Based primarily on observations of communally roosting European Starlings, the "patch-sitting hypothesis" integrates DAC-based foraging behavior into an alternate explanation for communal roosting behavior (Caccamise and Morrison 1986). Early in the roosting season DAC-based starlings forage almost entirely on their DAC's where they prefer substrates providing soil invertebrates (e.g., managed lawns, pastures; Fischl and Caccamise 1986). Night-time roosts are usually near the DAC and are small (25–500 birds). As the season progresses towards the seasonal peak in numbers of roosting birds (mid to late August, Caccamise et al. 1983), starlings increasingly frequent larger, more distant roosts. The diversity of foraging habitats also increases, and the diet changes with the inclusion of far greater proportions of plant materials (fruits, seeds, Fischl and Caccamise 1985, 1986). The commute between DAC and roost plays a key role in the change in diet. This is because DAC's always contain foraging substrates suitable for collecting invertebrates (e.g., lawns), but they often hold no apparent alternate foraging substrates. For example, suburban neighborhoods and pastures are habitats where starling DAC's are common, yet they clearly offer little by way of sources for the plant foods that become important later in the season. When starlings commute between DAC's and distant roosts, they often make foraging stops at sites with particularly abundant food sources where they supplement their diet (e.g., fruiting trees, feed lots, grain fields). These supplemental feeding areas (SFA's) provide the bulk of the plant foods important late in the season (Caccamise and Morrison 1988). Despite dramatic changes in foraging substrates and the often long commuting distances (e.g., to 38 km, Wynne-Edwards 1929; 50 km, Hamilton and Gilbert 1969) common later in the season, starlings remain faithful to the same DAC where they return each day to spend most of the daylight hours.

The patch-sitting hypothesis is based on three assumptions: First, DAC fidelity provides benefits in addition to those associated with foraging there. Otherwise, there would be no reason to return to the DAC at times when birds travel to SFA's to supplement their diets. Though benefits of

DAC fidelity remain unclear, DAC-based roosting behavior appears widespread among communally roosting species (Morrison and Caccamise 1990). The second assumption requires that birds move to distant roosts in order to utilize high quality foraging sites (SFA's) located nearby. The third assumption is that birds use foraging areas (including SFA's) in ways that tend to minimize commuting distance. One expected outcome of the patch-sitting hypothesis is that a DAC-based bird would be expected to forage on its DAC so long as it is able to satisfy dietary requirements there. This leads to the prediction that foraging substrate quality should decline on DAC's as increasing proportions of the local roosting population become associated with large roosting congregations, i.e., when more individuals are leaving their DAC's to forage elsewhere.

In this study I tested this prediction by examining changes in foraging substrate quality on DAC's through the post-breeding roosting season of European Starlings. I evaluated changes in substrate quality by measuring feeding success on the most commonly used DAC-based foraging substrate. In my central New Jersey study area, managed lawns are the preferred foraging substrate on DAC's and are used throughout the post-breeding season (Fischl and Caccamise 1985). My goals were to: (1) identify factors contributing to the decline in use of lawns during late summer, and (2) determine the seasonal relationships between foraging success in lawn habitats and the formation of large roosting associations. I found a substantial seasonal decline in foraging success occurring at the same time that: (1) use of lawn habitats normally declines, and (2) starlings begin leaving their DAC's to forage and roost at distant sites. This outcome agrees with the prediction that foraging substrate quality declines when starlings leave their DAC's to forage elsewhere. These results, like some earlier tests (Caccamise and Morrison 1988), provide support for the patch-sitting hypothesis.

STUDY SITE AND METHODS

My study took place during the post-breeding roosting seasons (June–September) of 1984–1986 on and near the Rutgers Univ. campus in central New Jersey. I worked in the north-central quarter of same larger study area that has been used for several other recent studies of starling roosting and foraging (e.g., Caccamise and Morrison 1988). The area is a typical mixture of urban and suburban habitats (shrubbery, lawns, gardens) interspersed with small (mainly <2 ha) woodlots and agricultural fields. I sampled birds feeding only in managed lawn habitats, the most important habitat during the post-breeding season (Fischl and Caccamise 1985).

I recorded foraging behavior between 06:30 and 10:30 h by watching starlings through a car window with binoculars or a 20× spotting scope. Individual foraging bouts began when a bird attempted to feed (probed soil with bill) and continued until I recorded approximately 100 feeding attempts (probes), or until the bird flew away. Feeding bouts of <10 sec were

later removed from the data set. At the end of each observation, flock size, species composition and meteorological information were recorded.

I used a hand-held computer (Radio Shack TRS-80, Model PC-2) programmed to store time of day (±0.5 sec) and the keyboard character for each key depression. By coding individual keys for particular foraging activities, I was able to directly produce a computer-compatible data file from field observations. At the end of the day, I transferred the field data to a personal computer (IBM-AT) where a data base management program (dBASE III) performed initial calculations. Each activity was summarized (tally, mean duration and rate) over individual foraging bouts; these then became my sample units for statistical purposes.

I recognized five activities associated with foraging. (1) A *probe* consisted of a downward thrust of the bill into the substrate, presumably in an attempt to locate a food item. (2) A *successful feeding* followed a probe and was generally recognized by a very deliberate raising of the bill followed by a bobbing of the head, and generally a visible swallow. Or, when birds loaded several food items for nestlings, the items were manipulated in the bill, usually quite visibly, before foraging recommenced. *Feeding success* within each bout was represented by number of food items gathered per number of probes with the bill × 100. (3) *Handling time* was elapsed time from when a food item was first sought (probe) until it was swallowed. When birds loaded several items handling time ended when the bird resumed foraging. (4) Vigilant *scanning* occurred when a bird temporarily stopped foraging activities and raised its head in an apparent effort to search for potential danger. (5) I recorded all *aggressive acts* directed at nearby birds.

I used one-way ANOVA's to make comparisons among flock size classes and among 10-day sample intervals. For the latter, I used covariance analyses to evaluate main effects (10-day sample intervals) while holding constant the effect of a secondary variable (flock size). In both cases tests were preformed on untransformed data using the GLM procedure of SAS for personal computers. Mean comparison tests were performed using the Duncan's multiple range test (alpha = 0.05).

RESULTS

I evaluated a total of 553 foraging bouts of adult European Starlings feeding in lawn habitats. Bouts lasted an average of 3.5 ± 0.15 min and included a mean of 59 ± 2.9 probes each. The average probe rate was 16.9 ± 0.28/min and ranged from 0.5–40.0/min. Bouts often ended before 100 probes were recorded. Usually birds were frightened, but sometimes they left of their own accord. By including these shorter observations (>10 sec) in the analysis, I reduced the possibility of bias from over-representing birds foraging in the best sites, i.e., where they remained for the longest intervals.

Foraging behavior.—Seasonal changes in size of foraging flocks were indicated by significant differences among 10-day sample intervals ($F = 5.56$, $P = 0.0001$). Mean comparison tests revealed that size of foraging flocks generally increased through 29 August, and thereafter declined (Table 1, Fig. 1A). I was not able to detect seasonal patterns in either amount of total foraging time devoted to scanning (scan rate; $F = 1.29$, $P = 0.2212$) or aggression (aggression rate; $F = 0.71$, $P = 0.7414$). How-

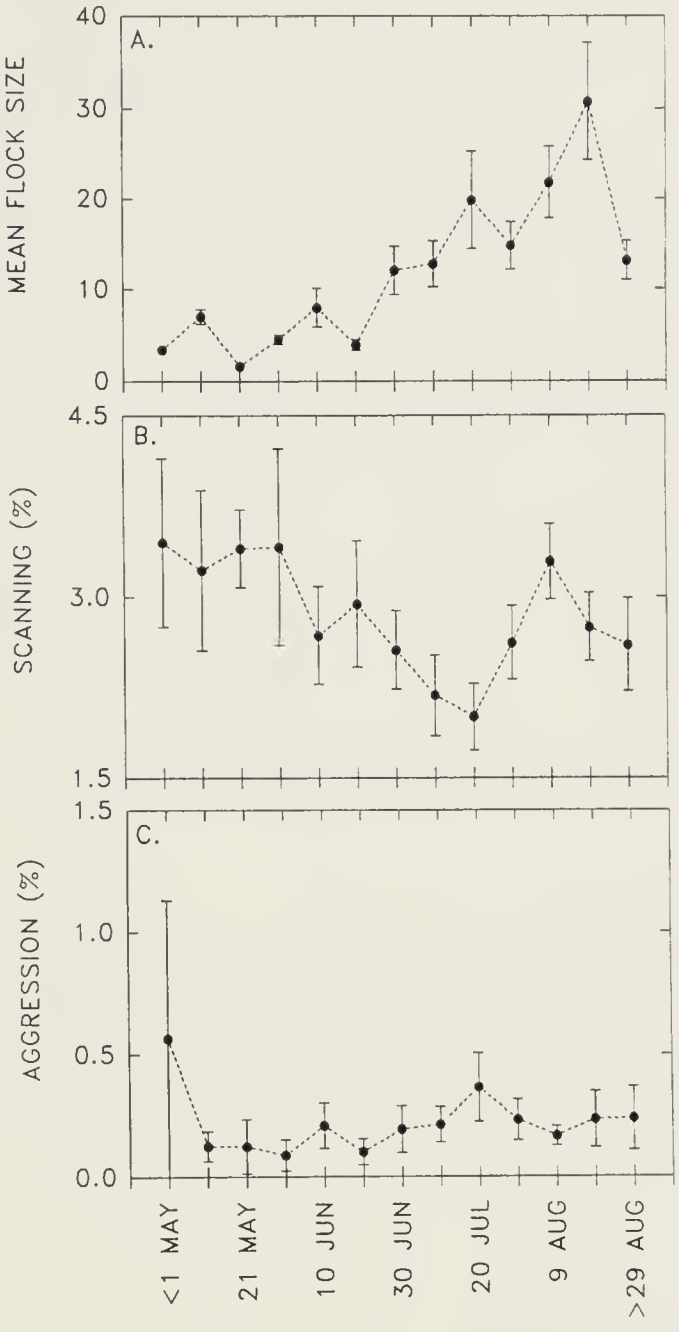

FIG. 1. Seasonal patterns in mean flock size (A), scan rate (B), and aggression rate (C) for European Starlings foraging on lawns. Dotted lines connect means, and vertical lines represent standard errors.

ever, during the earliest interval aggression rates were highly variable, and this may have masked actual elevated rates of aggression early in the season.

Flock size was related to other aspects of foraging behavior. A relationship was apparent between flock size and scan rate, however the response was not uniform over the full range of flock sizes (Fig. 1B, Fig. 2). Rather, highest scan rates occurred for solitary birds, while in larger

TABLE 1

COMPARISONS OF 10-DAY INTERVAL MEANS FOR GROUP SIZE AND HANDLING TIME (DUNCAN'S MULTIPLE RANGE TEST)

Flock size			Handling time		
Date	Mean	Duncan[a]	Date	Mean	Duncan
19 Aug.	30.7	A	10 May	4.7	A
9 Aug.	21.8	AB	19 June	4.0	AB
20 July	19.8	AB	20 May	3.5	ABC
30 July	14.7	B	30 May	3.4	ABC
29 Aug.	13.1	BC	20 July	2.7	BC
10 July	12.7	BC	9 June	2.6	BC
29 June	12.0	BC	30 July	2.6	BC
9 June	8.0	BC	30 April	2.5	BC
10 May	7.0	BC	9 Aug.	2.3	BC
30 May	4.5	BC	10 July	2.1	BC
19 June	3.9	C	29 Aug.	2.1	BC
30 April	3.4	C	19 Aug.	1.8	C
20 May	1.6	C	29 June	1.7	C

[a] Means for dates with the same letter are not significantly different at the 0.05 level of probability.

flocks scan rates seemed much lower. To examine this relationship I divided foraging flocks into size classes, and performed analysis of variance. I found significant differences in scan rates among flock size classes ($F = 4.43$, $P = 0.0001$). Mean comparison tests indicated that scan rates for solitary birds were significantly higher than for all other flock sizes. Despite the suggestion of a declining scan rate for flock sizes above one,

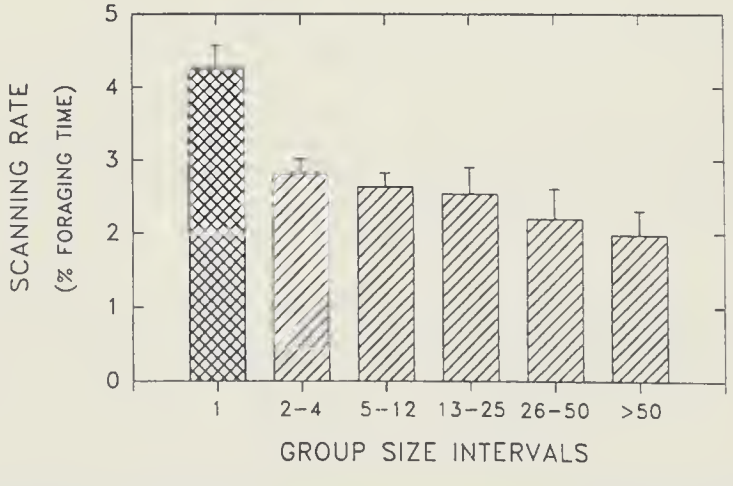

FIG. 2. Mean percent of total foraging time spent in vigilant scanning for each flock size category. Vertical lines on bars represent standard error, differing hatch patterns represent significant differences between means at 0.05% level.

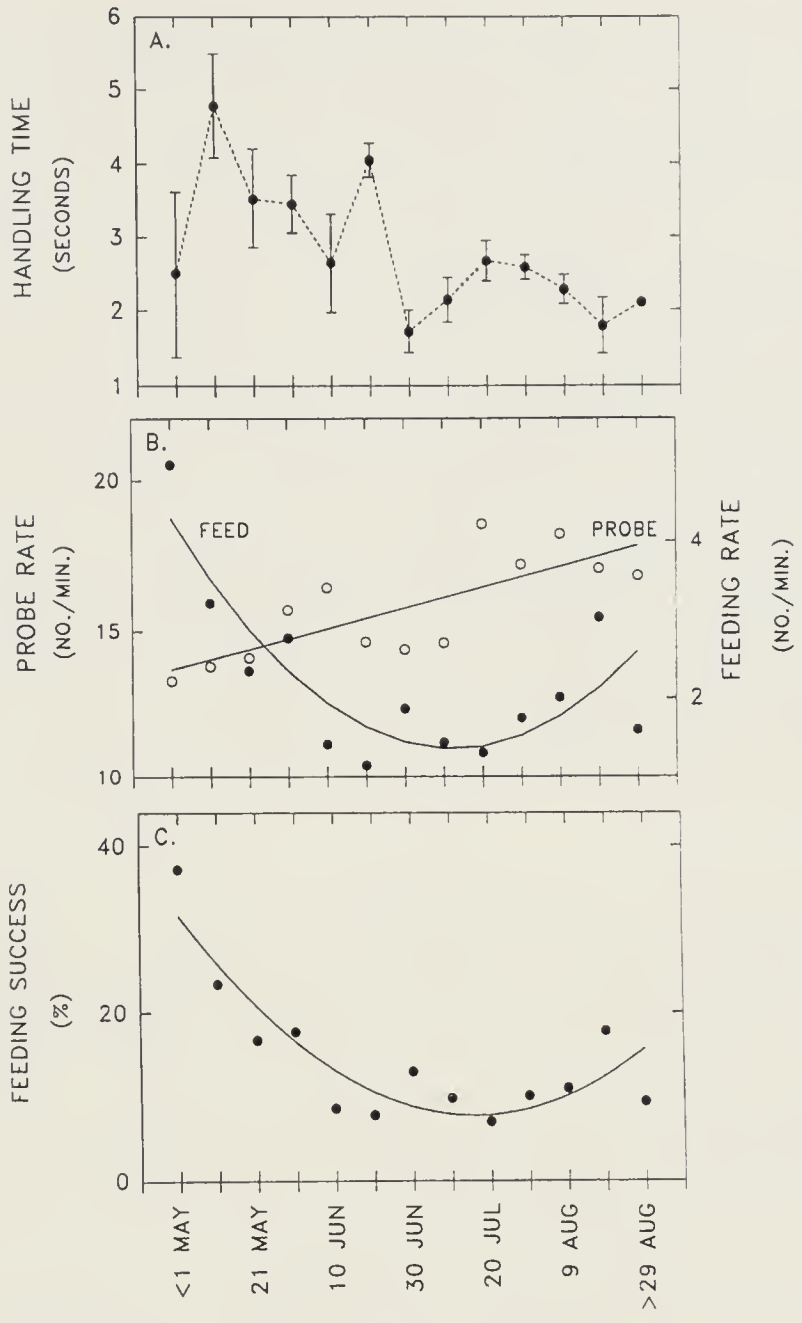

FIG. 3. Seasonal patterns in mean handling time (A), probe and feeding rate (B), and feeding success (C) for European Starlings feeding on lawns. Solid lines represent significant regressions (see text for equations).

mean comparison tests failed to detect any differences among the larger flock size categories (Fig. 2).

Rates of aggression were very low for the foraging starlings I observed, accounting for <0.3% of their total foraging time (Fig. 1C). I failed to detect significant differences in aggression rates among flock size classes ($F = 2.22$, $P = 0.0509$).

Foraging success.—Handling time varied significantly over the season

($F = 2.94$, $P = 0.0006$) with longer values occurring earlier in the season (Table 1). The short handling time of the earliest period was an exception, as such brevity was more typical later in the season (Fig. 3A).

I found significant differences among 10-day intervals for probe rate ($F = 3.35$, $P = 0.0001$), feeding rate ($F = 3.44$, $P = 0.0001$), and feeding success ($F = 3.12$, $P = 0.0001$). Probe rates increased significantly with seasonal advance ($Y = 12.98 + 0.35X$, $R^2 = 0.59$, $t = 4.01$, $P < 0.01$; Fig. 3B). However, feeding rates showed an overall decline with seasonal advance, although the response was not linear. Because feeding rates were lowest in middle to late July and higher towards both the beginning and end of the season, a second degree polynomial provided the best fit ($Y = 4.2920 - 0.0810X_1 + 0.0006X_2^2$; $R^2 = 0.73$; $t_{a1} = 4.8$, $P = 0.01$; $t_{a2} = 4.1$, $P = 0.01$; Fig. 3B). I combined responses of probe rate and feeding rate to arrive at an overall measure of feeding success. Feeding success was greatest early in the season, falling to its lowest levels in mid-summer, before rising again late in the season. Therefore, a second degree polynomial again best represented the data ($Y = 38.3 - 7.1X_1 + 0.4X_2^2$; $R^2 = 0.79$; $t_{a1} = -5.3$, $P < 0.01$, $t_{a2} = 4.4$, $P < 0.01$; Fig. 3C).

DISCUSSION

Foraging pattern.—Size of foraging flocks increased markedly through the season (Table 1, Fig. 1A). Others have reported similar seasonal changes for starlings (Williamson and Gray 1975, Fischl and Caccamise 1985). Enhanced predator protection through increased vigilance is a common explanation, although recent evidence suggests that individual risk may not always decline in larger flocks (Lindström 1989). Jennings and Evans (1980) found that time spent in vigilant behavior by foraging starlings decreased both as flock size increased, and as the location of individuals was nearer the center of the flock. I did not measure vigilance as defined by Jennings and Evans. In their study it represented intervals between my foraging bouts. They found that vigilance accounted for up to 50% of total foraging time. My measures of scan rate were much lower (3–6%), appearing more similar to their "head-up" display (4–5%). However, for this behavior they were not able to detect any relationships to flock size or position.

I found significantly higher scan rates for individual birds, although I did not detect differences among larger group size classes. The uniformly declining mean scan rates over the larger group size classes makes it tempting to speculate on a legitimate relationship. Nonetheless, variability inherent in visually measured behaviors of such short duration is difficult to manage, even with very large sample sizes. If such a relationship exists,

its detection will be easier with recorded media (e.g., film, video tape) where precision can be increased.

I found no effects for either group size or season on rates of aggression. Nonetheless, it is clear from Fig. 1C that variance in the earliest sample was much larger than the others. It is quite possible that this represents a real difference in behavior since starlings in the study area were still in relatively early stages of breeding during the first interval (Stouffer 1989). Failure to detect changes in rates of aggression would seem to preclude "despotic" (Fretwell 1972) monopolization of foraging resources on DAC's. This was the case even in late July and early August when group sizes were largest and foraging success on lawns was far below earlier levels.

Handling time tended to decline later in the season. The low values during the first 10-day interval may reflect the relatively high proportion of birds loading items for transport back to the nest. The nature of the data collection precluded separating these birds from individuals feeding for themselves; however the data were confounded in this way only during the earliest intervals. Nonetheless, beyond the first interval handling time declined significantly, indicating a change in the characteristics of food items being gathered. A decrease in average size of invertebrates taken would yield such a pattern.

The decline in feeding rate in late July and August represented an increase in search time between successful feeding encounters, likely resulting from a lower density of available invertebrates. Several studies have documented the transition in starling diets from mainly invertebrates in summer to largely plant foods in late summer and fall (e.g., Kalmback and Gabrielson 1921, Dunnet 1955, Fischl and Caccamise 1986). Working in my study area, Maccarone (1985) attempted to relate changes in food abundance to this dietary transition. He worked in several foraging substrates, including lawns, but his results on invertebrate abundance in lawns were inconclusive. He did find lower soil moisture in late summer which may result in lower availabilities for certain moisture sensitive organisms (e.g., earthworms).

The higher probe rates in late July in combination with lower feeding rates resulted in a significant decline in feeding success (Fig. 3B, C). At its lowest levels in mid-summer, feeding success was three times lower than at the beginning of the season. Taken together with the shorter handling time (e.g., smaller items), this represents strong evidence that quality of lawn as a foraging substrate declines during the mid-summer interval when starlings are most actively engaged in roosting and foraging away from the DAC.

Foraging success and use of distant roosts.—Though DAC-based roosting behavior appears widespread among communally roosting species,

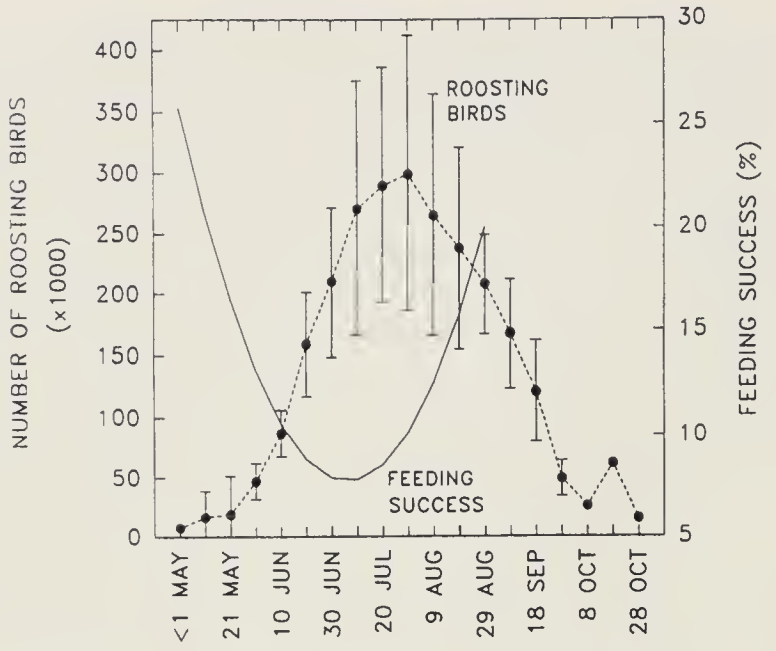

FIG. 4. Mean size (taken over four years) of total roosting population within 1000 km^2 study area in relation to a regression of feeding success over the roosting season. Size of roosting populations adapted from Caccamise et al. (1983); vertical lines through means present standard error.

benefits of DAC fidelity remain unclear. DAC-based birds can save up to 50% of the costs of travel to distant feeding sites by roosting near these sites and feeding during the morning and evening commute (Caccamise and Morrison 1986). While this provides an explanation for how DAC-based birds use distant feeding sites efficiently, it provides no insight into why they return each day to their DAC. Benefits of DAC fidelity likely exceed those simply associated with foraging because starlings maintain ardent fidelity to their DAC even when foraging success diminishes and they travel long distances to forage at alternate sites. Nonetheless, each day they return to their DAC where they spend most of the daylight hours.

The seasonal change in size of roosting populations in my census area has been shown to approximate a bell-shaped curve, with small populations early and late in the season, and large populations during a mid-summer peak (Caccamise et al. 1983). Although it is assumed that the size of the local population of starlings is approximately constant through this period (June–October) the change in size of the roosting population is believed to result from birds moving between small, scattered roosts (early and late in the season) and large associations (mid-season). Because the small roosts (25–1000 birds) are difficult to detect and monitor on a large regional basis these roosts remain uncounted in censuses. Thus, as birds move between the small undetected roosts associated with DAC's to the large censused roosts associated with SFA's, measures of the roosting population change accordingly.

I calculated mean size of the roosting population in my study area over the four years for which data were available (Caccamise et al. 1983) and plotted these results in Fig. 4 along with the regression describing seasonal changes in feeding success (Fig. 3). The results show that feeding success reaches its lowest levels at just about the same time that number of birds using large roosting associations reaches its maximum. Furthermore, as feeding success begins to increase again near the end of July, size of the roosting population again decreases as birds leave the large associations to return again to the small roosts associated with DAC's. It is possible that the concurrence of these events is entirely coincidental. Yet, other changes in foraging-related behavior occur at the same time and are likely related to the processes; size of foraging flocks increase (Fig. 1A; Williamson and Gray 1975), foraging substrate preference changes (Fischl and Caccamise 1985), and diet progresses from mainly insectivorous to frugivorous and granivorous (Kalmback and Gabrielson 1921, Fischl and Caccamise 1986).

My results are consistent with the predictions that declining foraging substrate quality on DAC's occurs when roosting populations are largest, and that starlings leave their DAC's in order to improve their foraging opportunities. The patch-sitting hypothesis holds that formation of large communal roosts is a secondary effect resulting from passive convergence of many individuals near high quality food patches (SFA's) at times when DAC's do not provide adequate foraging opportunities. By roosting near distant foraging sites and feeding during morning and evening commutes, DAC-based starlings are able to minimize commuting costs (Caccamise and Morrison 1986) at times when foraging substrate quality in preferred habitats on DAC's is relatively low.

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HOUSE WRENS ADJUST LAYING DATES AND CLUTCH SIZE IN RELATION TO ANNUAL FLOODING

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ABSTRACT.—I examined timing of reproduction and productivity in box-nesting House Wrens (*Troglodytes aedon*) inhabiting three riverbank woodlands subjected to different levels of flooding. In years when the North Platte River flooded its banks submerging ground foraging substrates, dates of nest initiation and egg laying in two wren populations were delayed and nonsynchronized. In contrast, timing of breeding was unrelated to annual variations in water levels or spring weather in wrens occupying a riparian area buffered from flooding. Rates of nest predation were unlikely to influence timing of laying because they did not vary among years or between early and late nests in any locality. Initial clutch size declined seasonally in all populations and was smaller in years when breeding was delayed by flooding. At all localities, variation in numbers fledged from successful nests was related to interactions between year and laying date. Generally, more nestlings fledged from early nests because clutches were larger. In addition, early clutches lost fewer young than late clutches of equal size in the population most impacted by flooding. Greater fledging success may select for early laying and may explain higher laying synchrony in early years. *Received 15 Jan. 1990, accepted 27 Aug. 1990.*

The seasonal onset of breeding in birds is often delayed by unfavorable environmental conditions (Lack 1966). Average laying dates in many bird species shift from year to year in response to annual variations in spring temperatures (van Balen 1973), snow melt (Slagsvold 1976, Zwickel 1977, Hannon et al. 1988), wetland dryness (Davies and Cooke 1983, Afton 1984), and food availability (Kallander 1974, von Bromssen and Jansson 1980, Ewald and Rohwer 1982). Average clutch size is often smaller in years when the breeding season starts late (Perrins 1970, Murphy 1986, Perrins and McCleery 1989), and clutch size also typically declines in individuals within years as the breeding season progresses (Klomp 1970, Perrins 1970, Hussell 1972, Murphy 1986, Svensson 1986). Diverse relationships between clutch size and timing of reproduction have been documented (e.g., Bédard and LaPointe 1985, Dickinson et al. 1987), but few studies have examined the effects that unpredictable catastrophic events have on egg-laying dates and clutch size.

House Wrens (*Troglodytes aedon*) are abundant breeders in deciduous riverine woodlands of the north-central Rocky Mountains (Finch 1989a). Such riverbank woodlands experience spring flooding annually, with water

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flow levels that vary greatly from year to year. Periodic flooding can have a major impact on associated plant and animal communities (Ewel 1979, Hunter et al. 1987), on use of foraging habitats by birds (Powell 1987), and on abundance, breeding time, and reproductive success of bird species that feed or nest on the ground (Knopf and Sedgwick 1987, Cruz and Andrews 1989, Ohlendorf et al. 1989). House Wrens glean insect prey off substrates near the ground (Guinan and Sealy 1987, 1989), and habitat selection by wrens may be related to availability of foraging substrate near nest sites (Guinan and Sealy 1989). The submergence of foraging substrates and food supplies under high floodwaters of long duration is a severe disturbance that may affect timing of reproduction in House Wrens.

Box-nesting House Wrens were studied over a four-year period in three woodland areas exposed to different levels of flooding. Here, I compare spatial and annual variations in timing of nest building and egg laying in wrens to variation in water flow levels, climatic factors, and rates of nest predation. To determine if productivity was associated with egg-laying dates, I tested for differences in clutch size and rates of fledging between early and late nests.

STUDY AREA AND METHODS

Three study plots were established in May 1982 in streamside habitats in Carbon County, southeastern Wyoming, at elevations ranging between 2050 and 2250 m. One plot was established at Rock Creek, 5 km northeast of Arlington and about 70 km northeast of Saratoga, and two plots, named Foote Camp and Treasure Island, were spaced 34 km apart along the North Platte River near Saratoga. Woodlands on the three study plots were dominated by narrowleaf cottonwood (*Populus angustifolia*); a variety of shrub species, especially willows (*Salix* spp.); and herbaceous species. Shortgrass prairie interspersed with sagebrush (*Artemisia* spp.) bordered riparian woodlands. Vegetation composition of the study plots is described in greater detail in Finch (1989b).

The extent of flooding varied among plots and years. The proportion of nest-box sites (21–22 boxes/plot) surrounded by floodwater was used as an index to the amount of ground surface covered. Foote Camp, the plot at the lowest elevation (2050 m), experienced heavy overbank flooding by the North Platte River in 1983 and 1984, and less so in 1986, with water covering as much as 100% of the ground surface for up to three weeks. The Foote Camp plot had gradual bank slopes and was bounded on three sides by a forked river, which may in part explain high river overflow. Treasure Island, also on the North Platte River, was flooded with less water (about 30% of the plot's surface was submerged in 1983 and 1984, and about 15% in 1986) for a shorter duration, probably because the riverbank was high (1.5–2 m) and on one side of the study plot only. Rock Creek, a smaller stream at the highest elevation (2250 m), flooded in 1983, 1984, and 1986, covering 0–15% of the plot's surface with water during peak flows. The Rock Creek plot was 120 m west of the stream and was buffered from water overflow by a strip of land. Rock Creek was used as a regulated irrigation channel, and level of water flow was erratic throughout each spring and summer, reflecting amounts of dam discharge in addition to runoff levels.

Nest boxes on all three plots were mounted 2 m high on live deciduous trees >10 cm dbh. The sample size of boxes on each plot was limited by woodland size. Boxes were spaced

at 30–35 m intervals in grids conforming to the shape and size of the riparian corridor. Nest boxes were built of 1.7-cm-thick cedar, 14 × 14 × 28 cm in dimension, with 3.8-cm-diameter entrances and latchable top doors.

Status (empty or occupied) of box and progress of nesting attempts were determined by checking all nest boxes early in the afternoon every 2–4 days from mid-May to late August of 1983 through 1986. Only a few boxes were used by wrens twice during a single breeding season. Boxes were cleaned out at the end of each summer so that nests from prior years were not mistaken for new nests. Because individual male House Wrens frequently fill multiple cavities with twigs (Kendeigh 1941), the appearance of the first egg was used as an index to nesting. For true nests, the first appearance of nesting material was identified as the date of nest initiation. Dates of nest initiation and egg laying were converted to numbers of days after May 1. The number of days between the egg-laying date and the nest-initiation date was considered the period of nest construction. Effects of the two factors, YEAR (1983, 1984, 1985, 1986) and PLOT (Foote Camp, Treasure Island, Rock Creek), were determined using two-way ANOVA's to test for temporal and spatial differences in dates of egg laying. The standard error of egg-laying date was used as an index of nesting synchrony. With regard to those boxes used twice in the same season, "second" nesting attempts were excluded from ANOVA's of egg laying because box reuse by the same pair of unmarked House Wrens could not be distinguished from late box settlement by a new pair.

Total annual precipitation, and mean minimum, mean maximum, and overall temperatures in May of each study year were computed from meteorological data collected at Saratoga, located 13 km southeast of the Foote Camp plot and 21 km northwest of the Treasure Island plot, and at Elk Mountain, 14 km northeast of the Rock Creek plot. Topography was relatively constant between field sites and matching weather stations, and therefore, I am confident that weather data at stations reflected weather at study plots. In contrast, even though the Elk Mountain and Saratoga weather stations were only about 60 km apart, temperature and precipation data varied between stations owing to differences in elevation, slope exposure, and proximity to mountains. Water flow was measured at two stations: North Platte River above Seminoe Reservoir, near Sinclair, Wyoming, and Rock Creek above King Canyon Canal, North Arlington, Wyoming. Total flow levels (ha-m) and midweekly flow rate (m^3/s) from April to September of 1983 through 1986 are reported. Weather and water flow data were collected by Wyoming Water Research Center, Univ. of Wyoming, Laramie.

Because flood levels and weather factors varied by year, their effects may explain year-to-year variation in onset of reproduction. I ranked yearly weather data and water levels from high to low and compared these scores to mean annual dates of egg laying using Spearman's rank correlations (coefficients are labeled r_s) (Sokal and Rohlf 1981).

Reproductive outcome, a dichotomous variable (failure or success), was classified as successful if at least one offspring fledged from the nest. Nests were considered abandoned if adults no longer attended the nest, and nest contents failed to hatch or fledge. Predation of whole clutches or broods was assumed if nests were empty before nestlings were due to fledge. Partial losses of clutches and broods resulted from egg-puncturing by intruders (probably other wrens; Kendeigh 1941; Belles-Isles and Picman 1986a, b; Freed 1986), hatching failure, and nestling starvation. Nests with reduced broods were considered successful if the remaining nestlings fledged. The difference in mean initial clutch size between successful and failed nests was assessed using ANOVA with the factors YEAR, PLOT, and OUTCOME entered concurrently.

Egg destruction by conspecifics and predation were the major causes of nest failure, accounting for 89% of 27 unsuccessful attempts (Finch 1990). I divided egg-laying dates into early and late periods and used contingency tables (OUTCOME × laying period) to

determine if frequency of nest destruction was dependent on timing of reproduction. Early and late periods were defined as dates before and after the mean date of egg laying each year for each stream. Outcome data from different years were combined if they were homogeneous or analyzed separately if they were heterogeneous.

To estimate timing and extent of brood losses, numbers of offspring fledged from each successful nest were subtracted from its initial clutch size. Wren clutches of unknown initial size were excluded from mean estimates of numbers fledged and lost from successful nests. To test for temporal and spatial variation in clutch size after egg laying and fledging, I analyzed the main and interaction effects of YEAR and PLOT using two-way ANOVA's. I also used two-way ANOVA's with factors YEAR or PLOT (depending on homogeneity of data), and laying period (early and late), to determine if clutch size, or numbers and rate (% clutch) that fledged, were related to timing of reproduction. To interpret seasonal changes in clutch size, pairwise comparisons among years were computed using Tukey's range test. I removed the effects of the factors PLOT and YEAR by computing case-wise residuals (listed by the MANOVA procedure, SPSS/PC+) and then used linear regression analysis to evaluate relationships between the residuals of laying date and the residuals of each dependent variable—initial clutch size of all nests, clutch size of successful nests, or numbers and percent of offspring fledged. To detect shifts in clutch size and fledging success with seasonal progression in laying dates, all early and late nesting attempts were included in analyses of clutch size and productivity.

All statistical analyses were performed using SPSS/PC+ programs (Norusis 1988a, b). A 0.05 probability level was used to test main effects and a 0.25 level to evaluate interaction effects in all applicable ANOVA's (Bancroft 1968). In tests with two or more factors, each effect was adjusted for all other factor effects using the default option, "classic experimental approach," in Procedure ANOVA. In analyses where interactions of PLOT and YEAR potentially masked relationships, I used one-way ANOVA's (or *t*-tests for pooled data) to reveal variation in laying dates, clutch size, or numbers fledged among plots by year or among years by plot.

RESULTS

Factors Affecting Dates of Egg Laying

Year and plot.—House Wrens generally began building nests in boxes later in 1983 and 1984 than in 1986 and, especially, 1985 (Fig. 1). Mean dates of nest initiation were earliest in 1985 on all three study plots, with the earliest nest found on 17 May 1985 at Foote Camp. Mean period of nest building in House Wrens ranged from a high of 13.3 ± 5.1 days at Treasure Island in the first study year to a low of 5.0 ± 0.3 days at Treasure Island in 1986. The earliest clutch found during the 4-year period was initiated on 22 May 1985. Variation in mean date of egg laying (after May 1) reflected the variation in mean date of nest initiation (Fig. 1). To eliminate problems associated with analyzing correlated variables (Beal and Khamis 1990), I report statistical comparisons of egg-laying dates only.

Mean laying dates varied among years ($F_{3,75} = 9.66$, $P < 0.0001$, N = 87) but not among plots ($F_{2,75} = 2.70$, $P = 0.075$). Based on results of one-way ANOVA's, annual laying dates varied at Foot Camp ($F_{3,22} =$

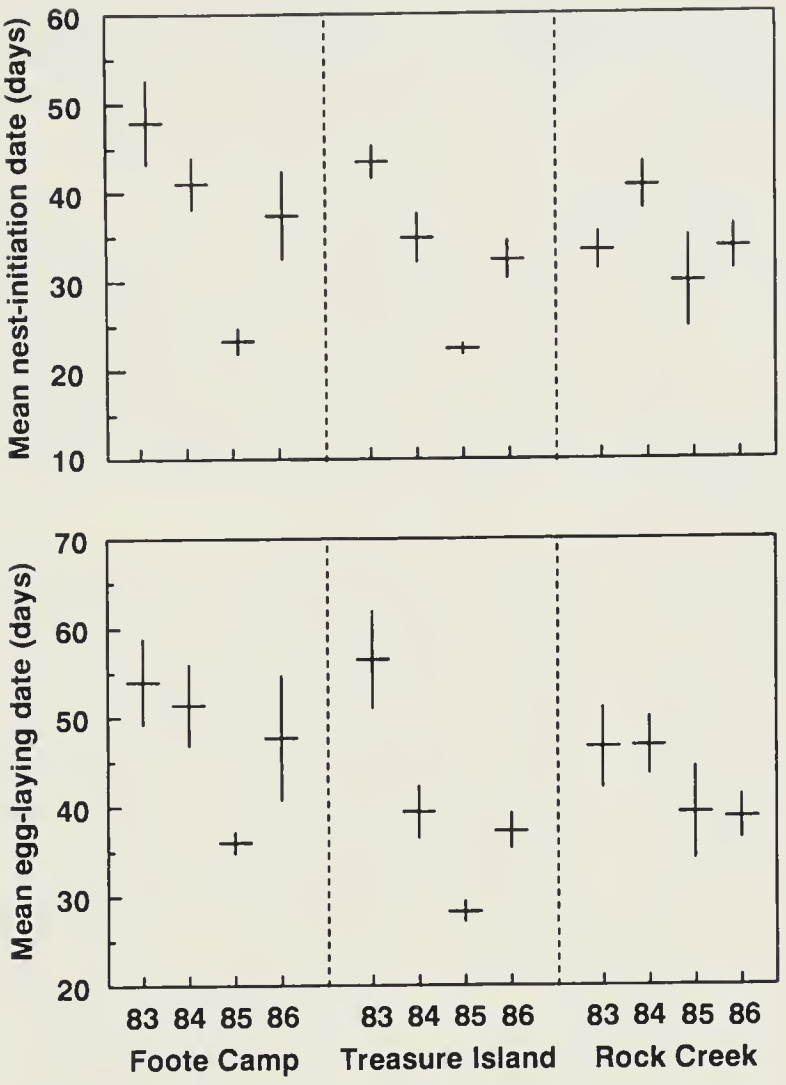

FIG. 1. Mean dates (±SE) of nest initiation and egg laying from 1983 through 1986 in three populations of House Wrens. Dates are days after May 1.

5.97, $P = 0.004$) and at Treasure Island ($F_{3,22} = 8.13$, $P = 0.001$) but not at Rock Creek ($F_{3,22} = 1.28$, $P = 0.297$). The importance of PLOT main effects may have been masked by the interaction of PLOT and YEAR ($F_{6,75} = 2.08$, $P = 0.066$). By analyzing plot variation by year, differences in mean laying dates among plots were exposed (one-way ANOVA: $P < 0.05$). Directional trends in mean laying dates were similar between the two plots on the North Platte River (Fig. 1), but these trends did not resemble the annual pattern in laying dates at Rock Creek.

Flooding and weather.—Declines in mean dates of laying from 1983 through 1985 were apparent in the North Platte River areas (Fig. 1). Laying dates were earliest at Foote Camp and Treasure Island in 1985, which may be related to low water levels of the North Platte that spring (Fig. 2). Water flow of the North Platte River was lowest in 1985, and

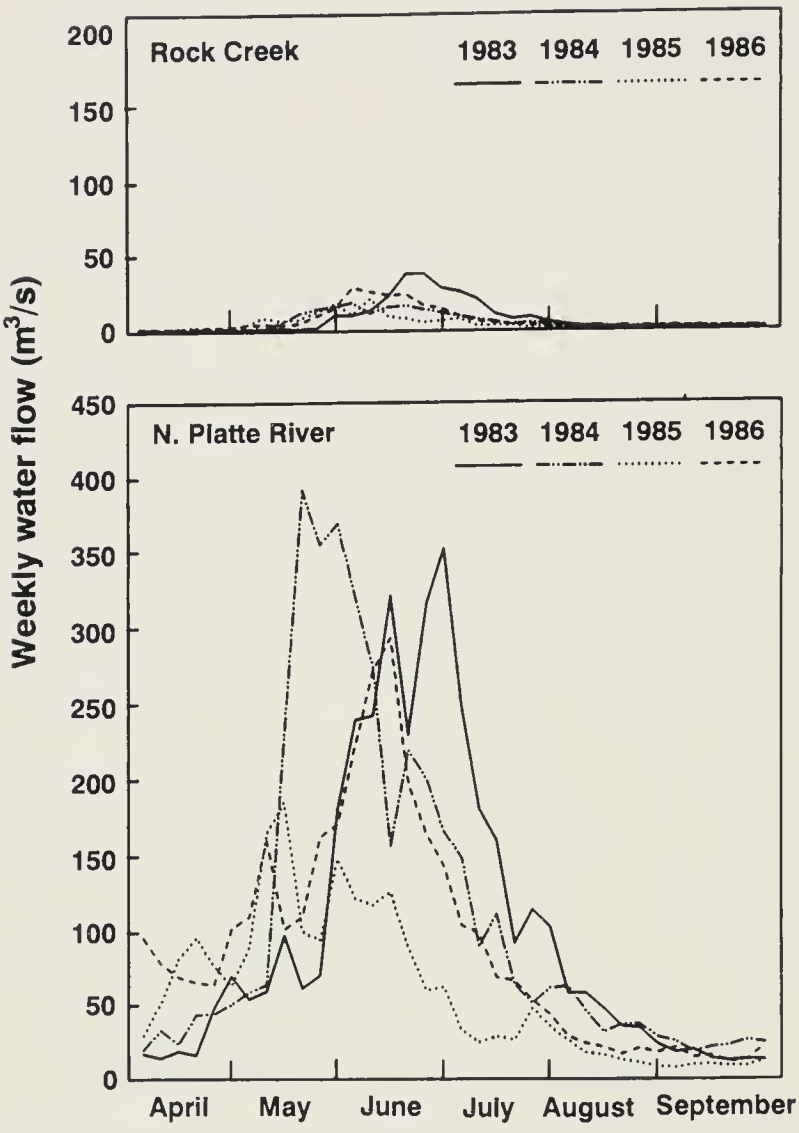

FIG. 2. Weekly water flow (m^3/s) from 1983 through 1986 of two streams adjacent to woodlands used by breeding House Wrens.

the two plots on the North Platte did not experience the heavy floods typical of the other three study years. In contrast, total water flow of the North Platte and Rock Creek peaked in 1983, the first study season. Some of the latest clutches on all three study plots were laid in 1983. However, wrens may have delayed egg laying in 1983 if this first study year was a transition period for learning about and adapting to nest boxes (see Finch 1989b). Nevertheless, water levels of the North Platte were also high in 1984 and less so in 1986, and again, egg laying at Foote Camp and Treasure Island was later than that in 1985.

Mean dates of egg laying (ranked by year) at Foote Camp and Treasure Island were perfectly and positively correlated ($r_s = 1.0$) with level of water flow of the North Platte River, but timing of nesting at the Rock Creek plot was not related to water levels of Rock Creek (Table 1). In

TABLE 1

SPEARMAN RANK CORRELATIONS (r_s) COMPARING WEATHER AND WATERFLOW FACTORS TO MEAN DATES OF EGG LAYING IN HOUSE WRENS

Variable	Foote Camp (N = 4)	Treasure Island (N = 4)	Rock Creek (N = 4)
Total waterflow (ha-m)	1.00**	1.00**	0.00
Mean temperature (°C)	−0.40	−0.40	0.40
Minimum temperature (°C)	−0.40	−0.40	0.20
Maximum temperature (°C)	−0.80	−0.80	0.40
Total precipitation (cm)	1.00**	1.00**	0.40

** $P < 0.005$.

general, mean laying dates at Foote Camp and Treasure Island followed dates of peak water flow of the North Platte River. That is, the average clutch in any year was laid after flood waters started to recede. For example, in the late flood year of 1983, mean laying dates at Foote Camp and Treasure Island were June 23 and June 26, respectively, following an initial peak in water flow on June 13. Likewise, a peak in water flow on 26 May 1984 preceded mean laying dates of 20 June at Foote Camp and 4 June at Treasure Island; a 12 May 1985 peak in flow preceded mean laying dates of 5 June and 26 May; and an 11 June 1986 peak preceded the mean laying date of 17 June at Foote Camp, but not the 6 June laying date at Treasure Island. Laying dates were unrelated to overall mean temperature, mean minimum temperature, or mean maximum temperature at any plot (Table 1).

Standard error in the date of clutch initiation was positively correlated with mean laying date at the Platte River plots ($r_s = 0.86$, $P < 0.001$, N = 8), indicating higher synchrony in low-flood years when nesting was early. Timing of reproduction at Rock Creek was generally less consistent within each breeding season than at the Platte River plots (Fig. 1), and standard error in laying dates was unrelated to mean laying date at this plot ($r_s = 0.20$, $P > 0.05$, N = 4). Caution should be used in interpreting the lack of a relationship between laying dates and standard errors at Rock Creek because the standard errors for any given year at Rock Creek may have been influenced by small sample size.

Timing of reproduction at plots on the North Platte River was also positively related to total annual precipitation (Table 1). Flood levels correspond to levels of spring runoff from snowmelt which are closely linked to total precipitation (i.e., amount of snowpack). Flood levels were perfectly and positively correlated to total precipitation at the North Platte River ($r_s = 1.00$, $P < 0.01$, N = 4). If precipitation rather than flooding

influenced timing of reproduction at the North Platte River plots, then onset of breeding should similarly be related to precipitation at the Rock Creek plot which was buffered from flooding (i.e., results are not confounded by flood effects). But mean dates of egg laying at Rock Creek were not associated with total precipitation (Table 1). Therefore, the relationship between delayed reproduction and increased precipitation at the Platte River plots may be an incidental outcome of the relationship between flood levels and precipitation.

Relationship Between Timing of Reproduction and Productivity

Frequency of nest failure.—Rates of nest failure were similar among years at each study area ($P > 0.05$) but differed among plots ($\chi^2 = 8.6$, df = 2, $P = 0.014$) so data were combined across years and analyzed by plot. The probability of nest destruction was greater at Foote Camp (44.4% of 27 nests) than at Treasure Island (8.0% of 25 nests), but both these probabilities were not statistically different from that at Rock Creek (30.6% of 36 nests). Early nests were lost at comparable rates among areas ($P > 0.05$), but late nests were more likely to fail at Foote Camp than at the other plots ($\chi^2 = 5.7$, df = 2, $P = 0.05$). At each plot, however, early nests were as likely to be destroyed as late nests ($P > 0.05$).

Initial clutch size.—Initial clutch size in House Wrens ranged from 3 to 10 eggs with an overall mean (±SD) of 6.2 ± 1.5 (N = 93) and a mode of 6 (33% of 93). Mean clutch size was similar among woodlands ($F_{2,81} = 2.41$, $P = 0.096$) but varied by year ($F_{3,81} = 3.68$, $P = 0.015$), reaching a maximum seasonal average of seven eggs at the Platte River plots in 1985 (Table 2), the year of minimum flooding. Main effects of plot may

TABLE 2

MEAN CLUTCH SIZE OF HOUSE WRENS LAYING EARLY AND LATE EACH YEAR ALONG TWO STREAMS

Laying period	N	1983		1984		1985		1986	
		$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
North Platte River									
Early	28	7.3	1.5	5.6	1.3	7.0	1.5	5.8	1.2
Late	27	4.0	0.9	5.3	0.8	7.0	1.0	5.3	2.2
Total	55	5.7	2.1	5.4	1.0	7.0	1.2	5.6	1.5
Rock Creek									
Early	24	7.2	1.1	7.1	1.4	7.2	0.8	6.0	1.2
Late	14	6.3	1.2	5.5	0.6	6.3	0.5	6.0	1.7
Total	38	6.9	1.1	6.6	1.4	6.8	0.8	6.0	1.3

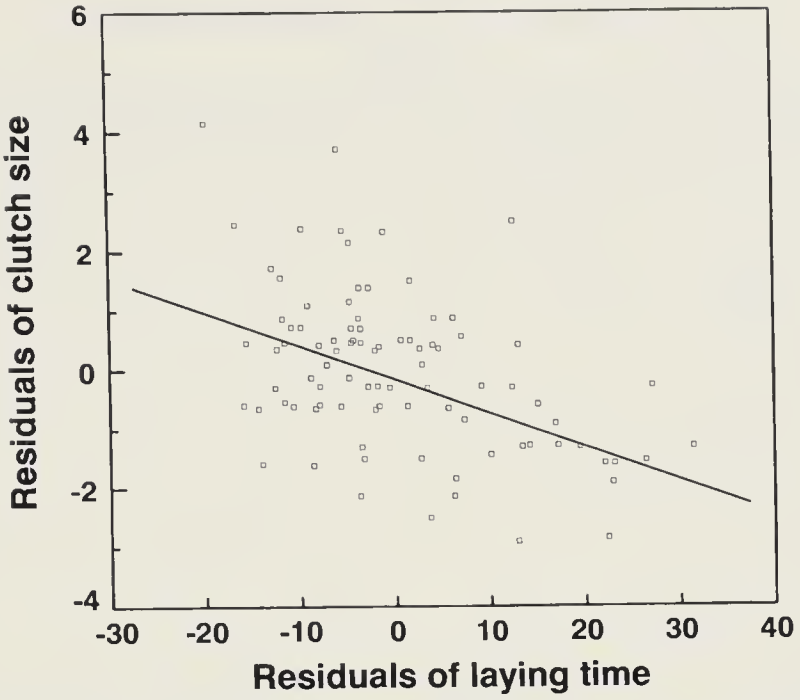

FIG. 3. Relationship between residuals of clutch size and residuals of laying time in House Wrens after PLOT and YEAR effects were removed.

have been masked by interactions between PLOT and YEAR ($F_{6,81}$ = 1.65, P = 0.145). In within-year comparisons, however, clutch size did not differ between the two Platte River plots (t-tests by year: $P > 0.05$).

To test the relationship between clutch size and laying period, the homogeneous data from the two Platte River plots were combined and analyzed separately from the Rock Creek data. Overall mean clutch size (adjusted for YEAR effects using ANOVA) varied between early and late clutches in House Wrens along the North Platte River ($F_{1,47}$ = 8.49, P = 0.005). Interactions between laying time and YEAR affected clutch size at the North Platte River plots ($F_{3,47}$ = 4.70, P = 0.006), with early clutches having more eggs than late clutches in 1983 and 1986 (Tukey's test: $P <$ 0.05), but not in 1984 and 1985 (Table 2). At Rock Creek, early clutches were generally larger in size than late clutches ($F_{1,30}$ = 5.08, P = 0.032) (Table 2), but interactions between laying period and YEAR were not significant ($P > 0.25$). When nests from different plots were pooled, the relationship between residuals of clutch size and laying dates (YEAR and PLOT effects removed) was negative ($r = -0.44$, $P < 0.0001$, N = 93) (Fig. 3).

Mean clutch size was 5.6 ± 1.5 eggs in failed nests (failure: 26% of 93 nests), and 6.4 ± 1.4 eggs in successful nests (success: 74% of 93). Successful nests had larger initial clutches than those that failed ($F_{1,72}$ = 13.07, P = 0.001) (adjusted for PLOT and YEAR effects). Clutch size residuals

TABLE 3

F-VALUES FROM TWO-WAY ANOVA'S INDICATING WHETHER THE NUMBERS AND PERCENTAGES OF YOUNG FLEDGED PER SUCCESSFUL CLUTCH DIFFERED AMONG YEARS AND BETWEEN EARLY AND LATE PERIODS OF EGG LAYING IN HOUSE WRENS

Factor	df	Fledged	% Fledged
Foote Camp (N = 16)			
Year	3	0.69	1.39
Laying	1	8.55*	6.85*
Laying by year[a]	3	4.23*	6.15*
Treasure Island (N = 24)			
Year	3	0.54	1.57
Laying	1	3.03	2.10
Laying by year[a]	2	3.95*	5.29*
Rock Creek (N = 29)			
Year	3	2.46	1.90
Laying	1	1.27	0.23
Laying by year[a]	3	3.00*	0.76

* $P < 0.05$.
[a] Interaction effects.

(YEAR and PLOT effects removed) were negatively related to laying time in successful nests ($r = -0.52$, $P < 0.0001$, N = 71), whereas clutch size and laying time were not associated in failed nests ($r = -0.35$, $P = 0.117$, N = 21). In sum, successful clutches were larger in initial size than failures, and these larger clutches were laid earlier in the season.

Successful fledging.—The number of young fledged from each successful nest ranged from two to eight wrens with a mean (±SD) of 5.2 ± 1.5 (358 of 440 eggs, 81%). Numbers fledged per successful nest were similar among years and in PLOT by YEAR interactions ($P > 0.25$) but varied by PLOT ($F_{1,46} = 4.84$, $P = 0.033$, N = 69). Fledging rate (% fledged/clutch) varied by PLOT ($F_{1,46} = 10.24$, $P = 0.002$) but was not affected by YEAR, or by PLOT by YEAR interactions ($P > 0.25$).

Although more young fledged ($r = -0.27$, $P = 0.025$) from earlier nests (residuals analyzed after PLOT and YEAR effects were removed using MANOVA), laying date explained only a small percentage of the total variation in numbers fledged (7%). Because offspring production from successful nests differed among plots, I analyzed data from each plot separately to determine if the relationship between productivity and laying date varied among plots. Because sample sizes were small per plot-year, these results should be regarded with caution. The influence of laying date on fledging success varied by year at Treasure Island (laying by YEAR

TABLE 4

MEANS AND PERCENTAGES OF YOUNG FLEDGED FROM EARLY AND LATE SUCCESSFUL NESTS OF HOUSE WRENS IN THREE RIVERINE WOODLANDS

Measure of productivity	North Platte River				Rock Creek	
	Foote Camp		Treasure Island			
	Early (N = 8)	Late (N = 8)	Early (N = 13)	Late (N = 11)	Early (N = 18)	Late (N = 11)
Fledge	5.5	4.6	5.0	4.1	5.9	5.6
	(0.8)[a]	(1.7)	(1.3)	(1.8)	(1.3)	(1.2)
Percent fledged	78.7	74.8	81.4	77.9	83.9	87.9
	(13.3)	(19.4)	(19.5)	(17.1)	(12.2)	(14.1)

[a] Standard deviations are in parentheses below each mean.

interaction, Table 3). Because early nests produced more young than late nests in some years, the overall trend at Treasure Island was a seasonal decline in fledging success (Table 4). Numbers fledged at Rock Creek displayed a similar trend (Table 4) and were also affected by interactions between laying date and YEAR (Table 3). At Foote Camp, however, numbers and percent that fledged varied between early and late nests (Table 3) with early nests producing more young (Table 4). The influence of laying date on fledging success at Foote Camp was also dependent on the year that the clutch was laid (laying by YEAR interaction, Table 3).

Clutch size in successful nests (plots and years pooled) was positively associated with the number of wrens that fledged ($r = 0.73$, $P < 0.0001$, N = 69). Hence, early clutches at Foote Camp produced more fledglings than late clutches because early clutches were larger. However, the relationship between clutch size and numbers fledged was stronger at Treasure Island ($r = 0.73$, $P = 0.0001$, N = 24) and Rock Creek ($r = 0.76$, $P < 0.0001$, N = 29) than at Foote Camp ($r = 0.57$, $P = 0.022$, N = 16). Because fledging rate was not correlated with clutch size at Foote Camp ($r = -0.11$, $P = 0.685$), the negative main effect of laying date on fledging rate detected at this plot only was independent of the collinearity between clutch size and numbers fledged.

Tests of the effects of laying date on rates of partial losses (% losses/clutch) were interchangeable, i.e., they generated the same statistical values, as tests of laying date effects on fledging rates. The average number of eggs or nestlings lost from nests that otherwise survived was 1.2 ± 1.1 offspring per clutch (83 of 440 eggs, 20%). Partial losses were absent at 21 successful nests, whereas three clutches were reduced by as many as four young (maximum lost: 67% of initial clutch). Reductions were higher (68 of 83 losses, 82%) during the incubation (plus hatching) period than

during the nestling stage. Also, in nests that remained active to fledging, larger clutches lost more young than smaller clutches ($r = 0.32$, $P = 0.008$, $N = 69$) (pooled across plots and years). Hatching failure and egg destruction by conspecifics accounted for most egg losses (Finch 1990), while nestling losses were due to starvation of young and predation during the time of fledging.

DISCUSSION

Timing of Reproduction

Mean dates of egg laying varied among years in House Wrens inhabiting woodlands along the North Platte River, but not in wrens occupying the Rock Creek area. Timing of reproduction on the North Platte River was strongly correlated with annual variations in levels of water flow of the North Platte. Overbank flooding of the North Platte occurred in years of high total precipitation, resulting in submergence of wooded land surfaces. Wrens forage on substrates near the ground (Guinan and Sealy 1987, 1989), and in this study, nested later in years when floodwaters rose in May and June, covering foraging substrates. Levels of water flow did not influence timing of reproduction at the Rock Creek site where overbank flooding was absent or minor compared to the North Platte River because of smaller stream size and greater distance of the stream from the nest boxes.

The peak period of water flow (mid-May to early July) overlapped the time when wrens were constructing nests, incubating eggs, and feeding nestlings. Annual and seasonal changes in water flow rates and water levels may directly influence availability, abundance, and hatching phenology of emergent insect prey. In heavy flood years, wren egg laying may be delayed if food shortages inhibit clutch formation, if nest sites are submerged under water, or if nest sites are unsuitable because adjacent habitat is flooded. As a consequence of late nesting, offspring will fledge in late July and August, when ground surfaces are drier and accessible for foraging, and drowning risks to offspring are reduced. On average, House Wrens along the North Platte River laid clutches in any year after seasonal peaks in water flow when flood waters began to recede. Hence, in areas where overbank flooding is severe and episodic, progressive seasonal rises and falls in water levels may serve as salient environmental cues for predicting the suitable time to breed.

Laying time was more synchronized along the North Platte River in 1985 when flooding was absent. Synchronized laying by many bird species may be common in years when early breeding is possible (e.g., Murphy 1986; Fig. 3, Hannon et al. 1988). The influences of other factors on

timing of egg laying were apparently more uniform and presumably more important than effects of flooding absence, allowing simultaneous early nesting by wrens in 1985. For example, early spring phenology as indexed by "warmth sums" (sum of number of degrees that mean temperatures reach above zero) is likely to favor early laying (Kluijver 1951, 1952; Murphy, pers. comm.), especially in years when potential impacts of disturbance factors are negligible. Local conditions may be more heterogeneous in years of heavy flooding if some habitat patches become suitable earlier than others. Also, response time may differ among females as flood waters recede if some are younger or less experienced in judging environmental conditions and the time to lay (Middleton 1979, Nol and Smith 1987), if body condition or fat reserves vary, or if a genetic component dictates timing of laying (Van Noordwijk et al. 1981).

Nest Failure, Clutch Size, and Fledging Rates

Nest predation increases through the breeding season in some bird species (Robertson 1973, Wiklund 1984) and declines over time in others (Findlay and Cooke 1982). It also varies from year to year (Myrberget 1986, Hannon et al. 1988) and from site to site (Murphy 1983, Picman 1988, Rotenberry and Wiens 1989). In this study, the probability of House Wrens fledging one or more young per nest varied significantly among riparian woodlands, but not among years. The frequency of nest failure did not differ between early and late nests at any plot, and therefore predation rates probably did not influence timing of breeding in House Wrens. Nest destruction by mammals, conspecifics, and possibly snakes was greatest at Foote Camp, the site where box occupancy rates were highest (Finch 1990), and late nests were more likely to fail at this site than at Rock Creek or Treasure Island. Seasonal and annual variation in predation rates may be more common when predators are abundant (e.g., Hannon et al. 1988), when predator or prey densities vary (e.g., Findlay and Cooke 1982, Angelstam et al. 1985), or when changes in plant phenology and habitat structure affect search efficiency of predators (e.g., Bowman and Harris 1980) or defense capability of prey.

Birds that lay early often have larger clutches than those that breed later in the season (Klomp 1970, Harvey et al. 1985, Murphy 1986). In this study, House Wrens laid larger clutches earlier in the breeding season in both geographical areas. Finke et al. (1987) also reported a seasonal decline in clutch size of House Wrens. My data were not sufficient, however, to test for the factors affecting within-season variation in clutch size. Clutch size may decline with season when individual females differ in age or experience (Curio 1983, Nol and Smith 1987), body mass or physical condition (Jarvinen and Vaisanen 1984), or genetic schedules (Van

Noordwijk et al. 1981). Individuals may adjust clutch size in response to seasonal and spatial heterogeneity in competition (Stutchbury and Robertson 1988), food supply (Greenlaw 1978, Hogstedt 1981), or territory quality (Hogstedt 1980), thus safeguarding their own chances of survival (Moss et al. 1981) while satisfying the feeding demands of their offspring (Perrins and Moss 1974, Nur 1986).

Late-nesting House Wrens with experimentally enlarged broods can raise additional chicks that weigh the same as those in broods of modal size (Finke et al. 1987). If offspring do not differ in survivorship before fledging as Finke et al. maintain, then House Wrens may adjust clutch size in relation to the probability of offspring survival after young leave the nest. Drilling and Thompson (1988) demonstrated that rates of return to natal sites were higher for House Wren chicks from early nests than for those from late nests. House Wrens fledging late have less time to develop, molt, acquire nutrient reserves, and learn survival skills before fall migration. A short developmental period before migration may explain reduced overwinter survival and lower recruitment rates of late-hatching chicks (Drilling and Thompson 1988, Hepp et al. 1989). To offset a seasonal decline in success resulting from low survival rates of late-fledging offspring, adult females may limit clutch size late in the season or in late years.

Mean clutch size fluctuates annually with mean laying date in populations subjected to environmental conditions that vary from year to year (Murphy 1986, Perrins and McCleery 1989). Spring weather and food supply are the extrinsic factors most frequently implicated as causes of yearly variation in breeding time and productivity of passerines (Perrins 1970, Hussell 1972, van Balen 1973). In this study, House Wrens along the North Platte River varied clutch size among years in relation to yearly shifts in laying schedules. In years when the North Platte River flooded its banks, laying was delayed and mean clutch size was smaller. In contrast, in the year when flooding was absent, clutches were large in both early and late nests apparently because late nests were earlier relative to other years. At Rock Creek, mean clutch size was similar among years, corresponding to the annual constancy in mean laying dates and the lack of flooding effects. Annual variation in clutch size in House Wrens may be related to year-to-year variability in conditions suitable for offspring survival, such that larger clutches are selected against in unfavorable years, e.g., late years of heavy flooding.

Laying larger clutches as early as environmental conditions allow has advantages for House Wrens. More nestlings fledged from early nests at Foote Camp, the plot most impacted by yearly variation in flooding. At all localities, seasonal differences in fledging success varied by year. In

years of delayed breeding, late nests produced fewer fledglings than early nests. Greater fledgling production was related to larger clutch size in early nests as well as to reduced rates of brood reduction. Rates of partial losses were less at early nests than at late nests, and as a consequence, early clutches fledged more young than late clutches of equal size. This may select for early laying and may explain the higher synchrony in laying dates observed at the North Platte River in early years.

Annual and within-season flooding inundates land surfaces with variable amounts of water which may affect food supply, food acquisition and delivery to young, and parenting abilities. Partial losses were caused by nestling starvation, egg destruction, and hatching failure. Seasonal changes in hatching failure may be related to variation in egg quality (Jarvinen and Väisanen 1983, 1984) resulting from seasonality in food value or availability, and physical condition of females. Increased rates of clutch/brood reduction later in the season may be associated with reduced food supplies (e.g., Hogstedt 1981) or early onset of winter weather. Also, late-nesting females are often young and inexperienced and may not be able to forage efficiently enough to produce high quality eggs or provision all their young (Perrins and Moss 1974, DeSteven 1978).

In my study areas, yearly fluctuation in flood levels appeared to be the most important extrinsic factor inhibiting the onset of reproduction in House Wrens. The catastrophic effects of flooding may have overshadowed the influences of other extrinsic factors. Alternate factors may operate more strongly in years when levels of water flow are low. Also, this study did not evaluate how intrinsic differences among individual females or males affect laying time or productivity. More data are needed to determine such effects. In this study, three populations of House Wrens responded to local and geographical variations in environmental conditions each year by adjusting laying date and clutch size. When environments are temporally variable and locally unpredictable, organisms may adjust reproductive effort relative to the probability of reproductive success (Williams 1966). Flexibility in reproductive effort, habitat use (Finch 1989a), and nest-site selection (Gutzwiller and Anderson 1987, Finch 1989b), as well as behavioral dominance in interspecific interactions (Belles-Isles 1986a, Finch 1990) may explain why House Wrens numerically dominate avifaunas in deciduous woodlands of the Rocky Mountains (Finch 1989c, Finch and Reynolds 1988).

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ROUTES AND TIMING OF MIGRATION OF FALCONS BANDED IN CANADA

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ABSTRACT.—We banded 6494 falcons, primarily (85%) in western Canada. Recovered falcons (235, 3.6%) included six Gyrfalcons (*Falco rusticolus*), 96 Prairie Falcons (*F. mexicanus*), 86 Peregrine Falcons (*F. peregrinus*), 44 Merlins (*F. columbarius*) and three American Kestrels (*F. sparverius*). Some Gyrfalcons, Prairie Falcons, and Merlins were recovered in Canada in winter. The migrating falcons generally moved through the North American interior. Prairie Falcons used two separate migration routes, one west of the Rocky Mountains and one east within grassland habitat. Recoveries suggest that Prairie Falcons did not fly the shortest distance to their wintering grounds. "Canadian" Prairie Falcons overlapped in their winter distribution with falcons banded at least 650 km south in Wyoming. Although widely dispersed outside of the breeding season, Prairie Falcons inhabited grasslands during migration and winter. Peregrine Falcons moved long distances, passing rapidly through Canada and the United States, and spent approximately seven months of the year outside of Canada along the Central American coasts and in South America. Some Merlins did not migrate. Sexual differences in the recoveries of Prairie Falcons could be attributed to differential mortality and not necessarily differences in migration. *F. p. tundrius* flew farther south than *F. p. anatum,* an example of "leap-frog" migration. Leap-frog migration was also suggested by one Merlin banded in the Yukon and recovered in Costa Rica. *Received 2 Jan. 1990, accepted 25 May 1990.*

We report here the banding and recovery locations of five species of falcons. Gyrfalcon (*Falco rusticolus*), Prairie Falcon (*F. mexicanus*), Peregrine Falcon (*F. peregrinus*), Merlin (*F. columbarius*), and American Kestrel (*F. sparverius*) were banded as part of toxicological studies and endangered species management (Fyfe 1976, Fyfe et al. 1976). In identifying the seasonal timing of movement, migration routes, and age and sex differences, we make a number of assumptions. First, we deduce the patterns of migration from banded falcons that were reported dead or captured alive. We assume that those falcons not encountered behaved similarly. Second, we assume that migratory behavior in these falcons is a heritable trait under the influence of natural selection, as it is in some other birds (e.g., Harris 1970, Berthold and Querner 1981). Third, we assume that the chance that a dead falcon was found did not vary throughout the year nor within an ecogeographic region (e.g., the North American Great Plains). However, differences may exist in the reporting rate of

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banded falcons between regions in North, Central, and South America based on human population density, nationality and habitat characteristics.

STUDY AREA AND METHODS

From 1967 to 1980, 6494 falcons of five species were banded in Canada under a master banding permit held by R. W. Fyfe. One recovered Gyrfalcon and 33 (38%) recovered Peregrine Falcons had been banded or released in central or eastern Canada (east of 90° longitude), but most Gyrfalcons and Peregrine Falcons were banded in the western Canadian Arctic and Subarctic. Eighty-nine (93%) Prairie Falcons, 29 (66%) Merlins and all three American Kestrels were banded in southern Alberta, the remainder in Saskatchewan. We categorized peregrines from north of the tree line in Canada as *F. p. tundrius,* those to the south as *F. p. anatum* (White 1968), and those on the Queen Charlotte Islands, British Columbia as *F. p. pealei.*

Most falcons (89–95%) were banded as nestlings, but some adults also were captured. Starting in 1974, Peregrine Falcons were equipped with color bands in addition to the standard metal leg bands. When a report of a banded falcon was received from the banding office, a questionnaire was mailed to the finder, requesting additional information on the condition of the falcon when found (freshly killed, partly decayed, fully decayed), the precise location, type of habitat and cause of mortality if known. For an analysis of timing of migration, we excluded recoveries of fully decayed falcons. In the case of 6 falcons which were reported partially decayed, we subtracted 30 days from a recovery date and proportionately less according to recovery latitude and season. Thirty-three Peregrine Falcons (38%) were raised in captivity and released into the wild. These were of *F. p. anatum* stock and were released in the boreal forest, parkland or eastern forest regions of Canada. For nestlings banded in the final third of the nestling period (approximately 80% of all nestlings), we assigned sex based on their size relative to nest mates and their age.

RESULTS AND DISCUSSION

Recovery rates.—A total of 235 of the 6494 banded falcons (3.6%) were recovered (Table 1). Many recoveries were near the banding site and provided little information about migration. Recovery rate varied among

TABLE 1

NUMBER OF FALCONS BANDED IN CANADA AND RECOVERED IN NORTH OR SOUTH AMERICA

	Gyrfalcon	Prairie Falcon	Peregrine Falcon	Merlin	American Kestrel	Total
Banded	301	3447	870	1419	457	6494
Recovered	6	96	86	44	3	235
(%)	(2.0)	(2.8)	(9.9)	(3.1)	(0.7)	(3.6)
Dead/injured	5	86	36	30	2	159
(%)	(1.7)	(2.5)	(4.1)	(2.1)	(0.4)	(2.5)
Live captured	1	9	36	14	1	61
Circumstances unknown	—	1	14	—	—	15

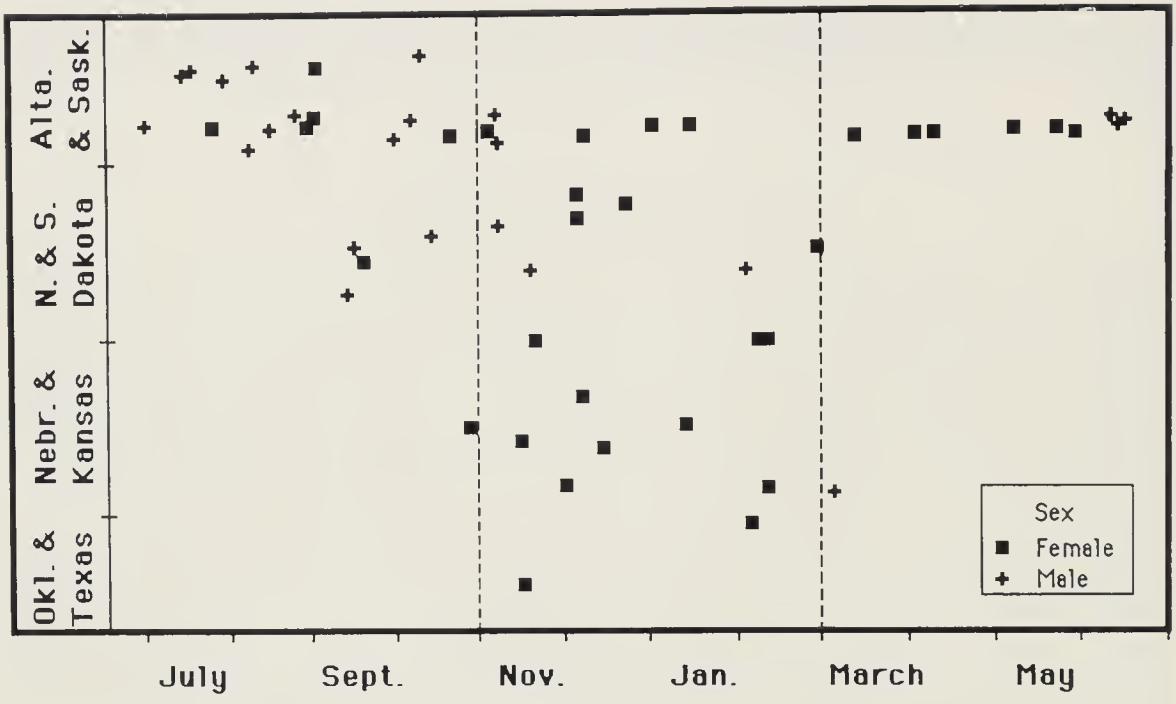

FIG. 1. Recoveries of male and female Prairie Falcons according to date and latitude. Broken, vertical lines delimit winter months (see text).

species from 0.7 to 9.9%. Thirty-six of the Peregrine Falcon recoveries were live captures, a result of the considerable trapping effort devoted to Peregrine Falcons (e.g., Ward and Berry 1972). When recaptured individuals were excluded the range of recovery rates narrowed to 0.4 to 4.1%. Even these recovery rates for dead falcons differed significantly between species ($\chi^2 = 19.61$, $P < 0.001$). Peregrine Falcons were most frequently recovered, possibly because they wore color bands. Kestrels were least frequently recovered presumably because their small bodies remained undetected more often than large falcons. Gyrfalcons had the second lowest rate, possibly because they frequented sparsely populated northern regions of Canada for most of the year. The observed rates of recovery were lower than those for raptors including owls banded in the United Kingdom, which ranged from 7–17% (Newton 1979:372). These differences probably reflect differences in encounter rates arising from differences in human population densities between Europe and the Americas, and only secondarily from differences in mortality rates.

Timing of migration.—Of six nestling Gyrfalcons, four were recovered between September and January, between 900 to 2400 km south or west of their nesting area. Two falcons were recovered near their nests. A sufficient number of Prairie Falcons, Peregrine Falcons, and Merlins had been reported as freshly killed, partly decayed or captured alive to permit an examination of the timing of migration. We defined the winter period for a species so that it encompassed those months in which at least 85%

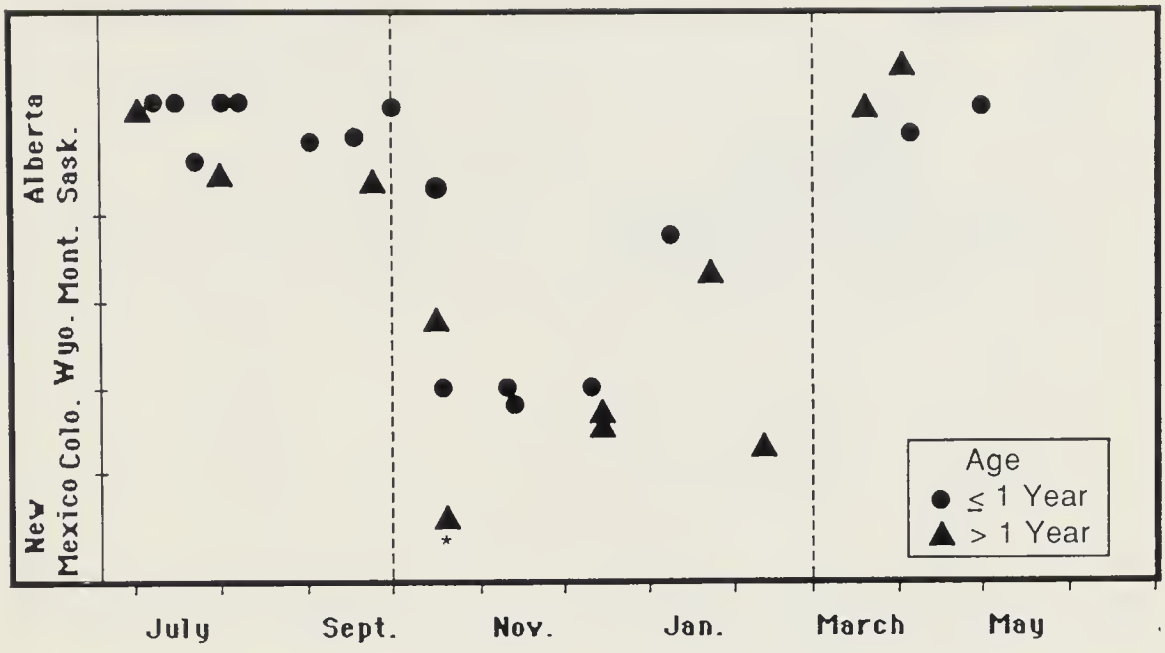

FIG. 2. Recoveries of adult and immature Merlins according to date and latitude. Broken, vertical lines delimit winter months (see text). One recovery in Costa Rica is indicated by a star.

of monthly recoveries were made from the southern half of the entire range of latitudes. For Prairie Falcons this period included November through February (Fig. 1), and for Merlins October through February (Fig. 2). For Peregrines this approach would have been misleading because the number of recoveries and questionnaires received apparently declined sharply once the falcons were south of the continental United States. A third order polynomial regression fitted to the recovery data suggests that the southward movement of these falcons stops between the months of November through March (Fig. 3).

One fledgling Prairie Falcon had moved 650 km to eastern Saskatchewan by mid August, but the southward movement did not occur until September (Fig. 1). Merlins departed from Alberta and Saskatchewan in September and October (Fig. 2). Peak migration, 90% of 105 captures, at Cape May, New Jersey, occurred between September 15 and October 15 (Clark 1985).

Peregrines departed from Canada during August through October (Fig. 3). Field observations suggest that Peregrines traverse southern Alberta between September 17 to October 3 (51 sightings over 16 years; Dekker 1984), Wisconsin, between September 22 to October 5 (61% of 360 sightings; Enderson 1965), and Assateague Island, Maryland, between September 17 and October 25 (1082 sightings; Ward et al. 1988). One *F. p. anatum* was captured along the south Texas coast in October and was shot 12 days later 600 km south. In spring Peregrines traverse Alberta

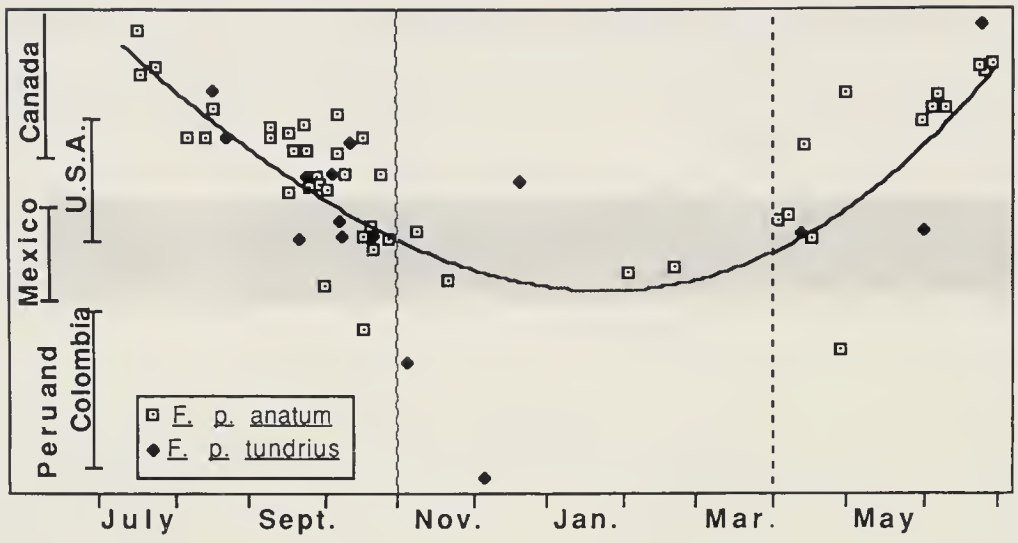

FIG. 3. Recoveries of *F. p. anatum* and *F. p. tundrius* according to date and latitude. Broken, vertical lines delimit winter months (see text) and stippling the maximum and minimum latitudes for Mexico.

between April 20 to May 3 (880 sightings; Dekker 1984). Six pairs of *F. p. tundrius* occupied territories in the Keewatin District of Canada's Northwest Territories by May 28, in each of three years (Court 1986).

For Prairie and Peregrine falcons, the species with a moderate sample of recoveries, migration appeared to progress more rapidly in spring than in autumn. The scatter of autumn recoveries suggests a lesser slope than the scatter of spring recoveries (Figs. 1 and 3).

Migration routes.—Ninety-six banded Prairie Falcons were recovered throughout the year from 0 to 1900 km from their natal or breeding sites (Fig. 4). Judging from the distribution of recoveries, Prairie Falcons used two migration routes and wintering areas. One route extended in a southeasterly direction, and another route southwesterly crossing the Rocky Mountains. To examine, in an *a posteriori* fashion, whether the Prairie Falcons moved southward in two distinct directions or in a broad band, we divided the recovery region in the United States into three parts. Of 28 Prairie Falcons recovered in the United States, none were recovered southeast of the Alberta banding area between longitudes 104 and 111°N (e.g., the eastern and western boundaries of Wyoming). This disparity was probably not caused by a bias in encounter and reporting rates, because eight of 17 other falcons reported from the western United States were found in this region ($\chi^2 = 16.03$, $P < 0.001$). Furthermore, Enderson (1964) saw wintering Prairie Falcons in this region.

Whether Prairie Falcons used an easterly or westerly route depended on their area of origin. Of 21 falcons that used the eastern grassland route, a greater proportion originated east of 111° longitude (N = 14) than west

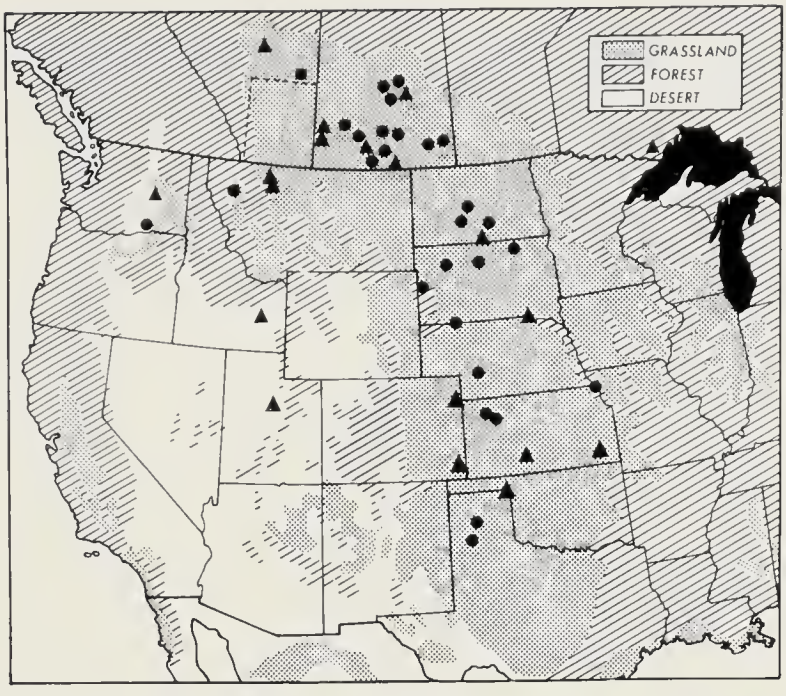

FIG. 4. Recovery locations of 48 Prairie Falcons are shown in relation to habitat and age. Circles represent individuals up to one year old, and triangles older individuals. Forty-eight additional individuals were recovered near their banding sites within the area bounded by a dashed line in southern Alberta. Of 96 falcons, nine were banded in Saskatchewan. Eighty-seven falcons were banded as nestlings and nine as adults.

of 111° longitude (N = 7). Of seven falcons that used the western route, six originated west of 111° longitude ($\chi^2 = 5.79$, $P = 0.016$).

Prairie Falcons that used the eastern migration route occupied habitat broadly categorized as grassland. Instead of flying directly southeast from Alberta, they apparently moved first due east into Saskatchewan and then south (Fig. 4). Once in the United States, 21 Prairie Falcons used a region ($\bar{x}$ longitude = 101°, SD = 3.3) similar to 44 Ferruginous Hawks (*Buteo regalis*) ($\bar{x}$ longitude = 103°, SD = 3.4) also banded in Alberta (Schmutz and Fyfe 1987). Both raptors used similar migration routes although their winter food habits are apparently very different. Horned Larks (*Eremophila alpestris*) are a primary winter food for Prairie Falcons (Enderson 1964, White and Roseneau 1970). Ferruginous Hawks probably rely on black-tailed prairie dogs (*Cynomys ludovicianus*; Schmutz and Fyfe 1987).

An affinity for grassland was also evident from the recovery locations of Prairie Falcons that moved southwesterly. Of seven individuals, five were recovered in or near grassland habitat even though this type of habitat is comparatively rare there. Only two Prairie Falcons were recovered in forest habitat; in western Ontario, and in the Black Hills of South Dakota.

Prairie Falcons banded in Alberta and Saskatchewan mixed extensively on migration and in winter with falcons banded in Wyoming. Although

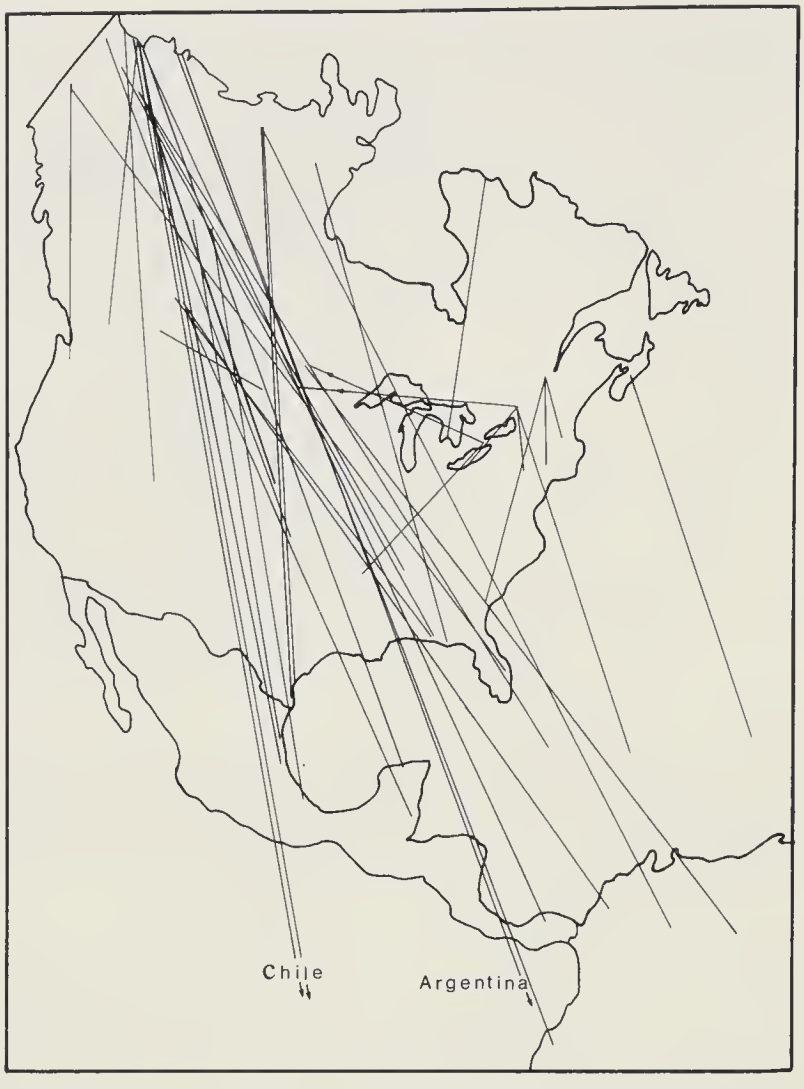

FIG. 5. Thirty-seven peregrine banding and their southerly recovery locations are connected via a straight line. Two northwesterly movements in North America are indicated by arrows. Three recovery locations near Iquique and Traiguén, Chile, and Neuquén, Argentina are not shown. Falcons live captured at the Texas (N = 8) and Maryland-Virginia coasts (N = 7) are also omitted.

27 Wyoming falcons (Enderson 1964) were banded at least 650 km south of where our 21 recovered falcons were banded, fall and winter recoveries did not differ along a north-south (Mann-Whitney $U = 258$, $P = 0.539$) nor an east-west axis ($U = 250.5$, $P = 0.605$). Seven of 27 Wyoming falcons recovered between October and February were actually found northeast of their breeding area, including two in Manitoba. Prairie Falcons banded in Idaho moved to higher elevations in late summer and also in a prevailing easterly direction. Seven of 13 recoveries/sightings were made east of the continental divide (Steenhof et al. 1984). Thus, few falcons from these subpopulations flew the shortest distance to their wintering areas. This suggests that vagrancy has advantages that outweigh

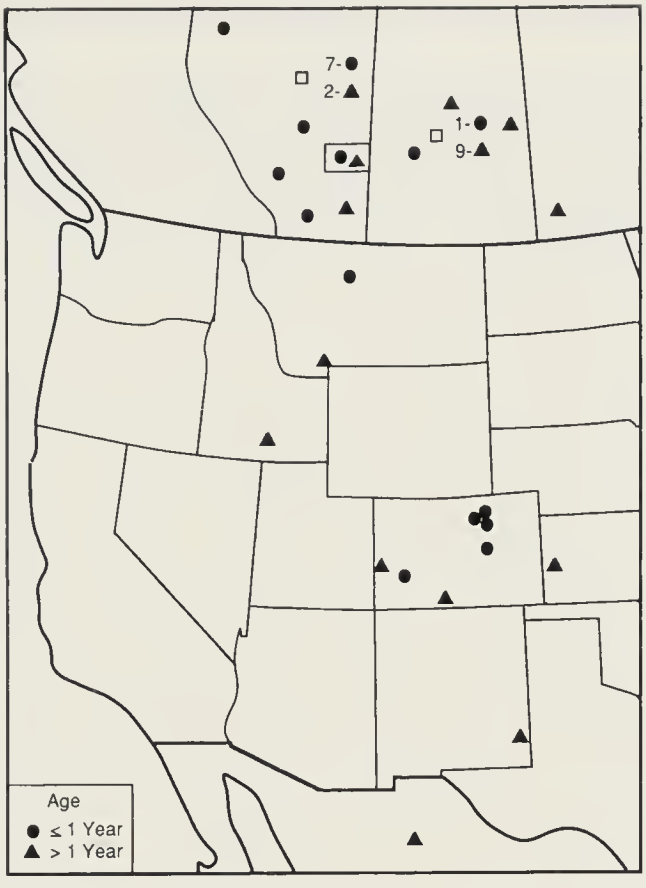

FIG. 6 Forty-three locations of Merlin recoveries are shown. Twenty-nine falcons were banded in southern Alberta, one near the Alberta boundary in southern Saskatchewan and 13 in the city of Saskatoon, Saskatchewan. One Merlin which was banded near the Arctic circle in the Yukon, was recovered in Costa Rica (not plotted).

the energetic cost associated with movement. Such vagrancy could result from falcons moving in random directions and stopping only when patchily distributed prey is encountered in abundance. Depending on the frequency of patches, some movements may be short, others long. Because of greater precipitation, grassland habitat may harbor prey in greater densities than desert-shrub habitat. This could explain the prevailing eastward movement.

A tundra Peregrine Falcon flew the longest distance. This falcon was banded at the mouth of the Mackenzie River in northern Canada and was recovered 12,000 km south near Traiguén in Chile. Most Peregrine Falcons were recovered southeast of their banding location (Fig. 5), although direction depended on where the falcons originated. Of 27 falcons from western Canada (W of 90° longitude) the movement was southeasterly with a mean of 137 degrees (SD = 17.4) from the banding/release site. The mean direction of eight falcons originating from eastern Canada was southwesterly with a mean of 226 degrees (SD = 47.4). One *F. p.*

pealei was recovered, in August, 200 km from its natal site in British Columbia.

Patterns of Peregrine migration were difficult to examine because of the different banding/release areas throughout Canada, the irregularly shaped continents, and two main methods of recovery, including live trapping at coastal beaches (e.g., Ward and Berry 1972, Henny et al. 1982) and reporting by the public. Nonetheless, several patterns are suggested by the data.

A Peregrine's affinity for coastal areas has been suggested by Enderson (1965), Bonney (1979), and by our data for the Central American coast (Fig. 5). Seven Peregrines were recaptured along the Atlantic coast in Maryland and Virginia. Recoveries suggest that northwestern Peregrines migrated over North American land masses but inhabited coastal regions in winter. During midwinter or the austral summer (November to February), 7 of 10 falcons were found within 60 km of coasts in Central and South America. Our band recovery data are of limited utility in assessing the degree of migration over sea, a route which some Peregrines are known to take (e.g., Kramer 1985). Not all coasts were used equally, however. Only one of our *F. p. anatum* was recovered near the Pacific Coast in North America. In South America no recoveries were reported from the South Atlantic Coast despite the occurrence of Peregrines there (Albuquerque 1984).

Thirty of 44 Merlins were found in Canada, 12 in the United States, 1 in northern Mexico and 1 in Costa Rica (Fig. 6). A cluster of recoveries in Colorado (6 of 11 U.S. recoveries) suggests that this region is an important winter area for the populations studied. Three individuals were recovered between Canada and Colorado, along the eastern edge of the Rocky Mountains in the United States. The banded Merlins were reared or breeding in the parkland habitat at the northern edge of the mixed-grass prairie, and were recovered in winter in the woodland habitat along the eastern foothills of the Rocky Mountains. Two Merlins banded in our banding region in 1930 and 1931 were recovered in Arizona (Lincoln 1936).

Of the kestrels banded in Alberta two were recovered again in Alberta and one in Michigan.

Falcon dispersion.—To examine the breadth of dispersion by falcons originating from Canada in relation to their respective species' winter range, we compared the distribution of recoveries with sightings made during Christmas bird counts (CBC) in 1981. We chose 1981 because at the close of this banding project the greatest number of banded falcons may have been alive. The recoveries used are those from the winter periods (Figs. 1–3).

TABLE 2

A COMPARISON BETWEEN THE NUMBER OF FALCONS COUNTED ON CHRISTMAS BIRD COUNTS AND THE NUMBER RECOVERED DURING WINTER (SEE FIGS. 1–3) IN THE WESTERN UNITED STATES. THE NUMBER OF FALCONS COUNTED IS REPORTED PER 1000 KM DRIVEN

	Km (×1000)	Prairie Falcon		Peregrine Falcon		Merlin	
		Counted	Recovered	Counted	Recovered	Counted	Recovered
Washington	10.7	0	2	0.6	0	4.1	0
Oregon	14.1	2.2	0	0.7	0	1.4	0
Idaho	4.3	7.9	2	0	0	0.7	1
California	46.7	3.1	0	0.6	0	1.2	0
Nevada	1.6	3.8	0	0.6	0	0	0
Utah	4.0	6.3	0	0	0	1.3	0
Arizona	8.0	6.1	0	0.1	0	1.4	0
Montana	7.0	2.4	2	0	0	0.9	2
North Dakota	6.1	0.8	1	0	0	0.5	0
South Dakota	5.1	0.8	3	0	0	1.0	0
Wyoming	4.5	1.8	0	0	0	0	0
Colorado	11.7	4.9	0	0	0	1.1	6
New Mexico	5.6	0	0	2.0	0	0.9	1
Nebraska	3.4	0	2	0	0	1.5	0
Kansas	4.3	6.7	4	0.5	0	1.2	1
Oklahoma	5.9	1.9	2	0.2	0	1.4	0
Texas	30.0	0.7	0	0.3	0	0.6	0
Total			18		0		11

Prairie Falcons were recovered in 8 of 17 states in the western United States (Table 2). The recoveries of Prairie Falcons by state did not differ significantly from the proportions suggested by CBC ($\chi^2 = 5.85$, $P = 0.054$, df = 2). In comparison to the small Canadian banding region, the vagrant falcons were spread over a recovery region that was many times larger. One Prairie Falcon exhibited remarkable winter site fidelity. This falcon was captured in Idaho in February at eight months of age and again 3 km away 12 months later.

Except for one *F. p. tundrius,* live-captured along the Virginia coast in December, none of our peregrines were recovered in the United States in winter. In comparison to Prairie Falcons, peregrines were rare on CBC in the western United States but were seen in nine of the 17 states shown (Table 2, see also Enderson 1965). These results suggest that most of the Canadian *F. p. anatum* and *F. p. tundrius* winter south of the contiguous United States.

Merlin recoveries were from five of the 17 states (Table 2). Merlins were seen on CBC in all but two of the western states, and the distribution of sightings differed significantly from the small sample of recoveries (χ^2

= 7.30, $P = 0.026$, df = 2). Six of our 11 recoveries were concentrated in Colorado, even though this state accounted for only 6% of all sightings (Table 2). Even if our banded Merlins, which originated from woodland habitat (aspen parkland), had restricted themselves to woodland habitat (Rocky Mountain foothills) on migration and in winter, their dispersion was narrower than may be expected based on available woodland habitat alone.

Migration versus residency.—Raptors as a group exhibit a diversity of dispersion patterns ranging from no migration to long distance movements (Newton 1979). Variability in the distance of migration, and partial migration by one sex or age group could be linked to food availability (e.g., Newton 1979).

Peregrine Falcons exhibited complete migration in this study in parallel with their waterfowl, shorebird, and songbird prey (Dekker 1984, Ward and Laybourne 1985). Gyrfalcons, Prairie Falcons, and Merlins exhibited partial migrations, consistent with the exodus of some avian prey from their arctic and subarctic environment, or the hibernation of mammalian prey (*Spermophilus* spp.). In winter, Gyrfalcons occupied previously used nesting areas and probably relied on Ptarmigan (*Lagopus* spp.) for food (Platt 1976, Poole and Bromley 1988). However, even falcons that remained in Canada moved some distance from their breeding or natal site. Four Gyrfalcons moved 900–2400 km prior to or during winter months. Gyrfalcon movements do not reach far south. This falcon was rarely recorded on CBC in the United States (<1% of 493 large falcons seen in 1981, Table 2) or in southern Canada (Houston 1985, Slater 1987, Wiseley and Pinel 1987). Six Prairie Falcons were recovered in Canada in winter 13–600 km ($\bar{x}$ = 288 km) from their nests. We have no evidence that any Prairie Falcons actually remained in or near their original breeding or natal area. Casual visits to our study areas in winter indicate that the falcons had left their nesting area. Horned Larks, a primary winter food for Prairie Falcons (Enderson 1964, White and Roseneau 1970), winter only in extreme southern Canada (Salt and Salt 1976). Non-migratory Merlins are common in cities in prairie Canada and rare in rural areas (James et al. 1987). Merlin abundance in cities has increased since 1975, and this increase has been linked to a rise in the abundance of the Bohemian Waxwing (*Bombycilla garulus*).

Age differences.—Raptor cohorts can exhibit "differential migration" (Terrill and Able 1988) according to differences in resource use (e.g., Kerlinger and Lein 1986). Since falcons obtain at least some of their prey through aerial pursuit, age-specific differences in wing shape and size (e.g., White 1968) may lead to different feeding strategies and hence different wintering areas. Ward and Laybourne (1985) found that adult peregrines

TABLE 3
RECOVERY OF FALCONS OF DIFFERENT SEX ACCORDING TO STAGE IN MIGRATION. TIME PERIODS CORRESPOND TO THOSE IN FIGS. 1 TO 3

	Late summer/ autumn	Winter	Spring/early summer	χ^2	*P*
Prairie Falcon					
Females	7	19	6	9.69	0.008
Males	14	5	4		
Peregrine Falcon					
Females	17	4	6	0.75[a]	0.784
Males	10	3	4		
Merlin					
Females	2	7	—		
Males	1	2	—		

[a] df = 1.

consumed a significantly greater proportion of shorebird prey on migration than did immature peregrines.

The distributions of recoveries of adult and immature Prairie Falcons and Merlins (Fig. 4) were similar at the regional level. For Prairie Falcons the sample of winter recoveries (November to February, N = 24) was sufficiently large to permit a statistical comparison. We found no significant deviation from random north-south dispersion between age classes (Wald-Wolfowitz $T = 13$, $P = 0.225$; Conover 1971). This is consistent with the field observations of White and Roseneau (1970) who found that immature falcons comprised 64% of 70 encounters (but see Enderson 1964). Our data were insufficient, however, to determine whether clusters of locally separate age groups existed within the broad winter range used by this species or whether differences in the proportions of adults to immatures existed between years.

During the summer period we received no recoveries from the southern portions of the species' ranges. This suggests that even though some individuals may not attempt to breed during their first summer, they undertook a return migration.

Sexual differences.—Variation in migration pattern between the sexes may arise from differences in the timing of a return migration (e.g., Ketterson and Nolan 1976) or from differences in resource use according to body size. Significantly more male Prairie Falcons were recovered in late summer and autumn than in winter and spring (Table 3). The sex ratio had changed sufficiently so that only five males were recovered in winter

compared to 19 females. White and Roseneau (1970) captured 32 females and only four males in north central Utah in winter, corroborating that the sex ratio is imbalanced. Although all five males were recovered in the northern half of the winter latitudes compared to 11 of 19 females, this difference was not statistically significant ($\chi^2 = 3.16$, $P = 0.076$). These results suggest that the north-south gradient in recoveries of male Prairie Falcons was due to a greater mortality among males in late summer, and not to a difference in dispersion according to sex.

There was no difference between the sexes in the recovery of peregrines by season (Table 3), nor in their dispersion. The proportion of males and females above the line depicting the average progress of migration over time (Fig. 3; 9 males, 14 females) was nearly identical to the proportion located below (8 males, 13 females).

"Leap-frog" migration.—In some populations of migratory raptors, members of a northerly breeding segment winter farther south than a southern segment (Wallin et al. 1987). Two merlins banded in this study were recovered south of the United States, one in northern Mexico and one in Costa Rica. This Costa Rican recovery was the only recovery of merlins banded in the boreal forest of northwestern Canada and suggests that these northern Merlins (*F. c. bendirei*; Godfrey 1966) fly over the breeding and wintering grounds of *F. c. richardsonii* and winter in Central and South America. Clark (1985) received recoveries of 18 Merlins from Florida and the Greater Antilles. Although these falcons were banded on migration at Cape May Point, New Jersey and their breeding area was not known, this corroborates that Central America is an important wintering ground for Merlins.

To examine potential differences on migration between subpopulations, we examined recoveries of members of different subspecies. *F. p. tundrius* migrated further south than did members of *F. p. anatum.* The average recovery latitude of 15 falcons found in Central or South America, or reported freshly killed during November through February in North America, was 17°N (SD = 17.4, N = 8) for *F. p. anatum* and 2°S (SD = 27.7, n = 7) for *F. p. tundrius.* Despite the near disappearance of the southern breeding *F. p. anatum,* the northern breeding *F. p. tundrius* have not significantly invaded the wintering range of *F. p. anatum* as would be expected if competition were a major factor in determining the winter location of the two subpopulations.

Peregrines breeding in Canada are outside of Canada for seven months of the year. Their annual distribution includes many countries which makes conservation management an international challenge. In the late 1970s and early 1980s, after the use of DDT was banned in North America, spring migrants returned from Latin America with significantly higher

concentrations of DDE than the concentrations with which fall migrants departed (Henny et al. 1982). This international residency may pose a greater threat to Canadian falcons which appear to migrate farther south (Fig. 3) than do falcons released in the continental United States. Only one of nine recoveries of falcons banded in the United States (Barclay and Cade 1983) was reported south of the continental United States.

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SOCIALITY AND ONTOGENY OF COLORATION IN THE BLUE-AND-BLACK JAYS

A. Townsend Peterson[1]

Abstract.—To test the hypothesis that heterochronic changes in color maturation act to integrate avian social groups, the relationship between social-group size and maturation rates of four morphological characters was analyzed in the blue-and-black jays (*Cyanocorax* spp., formerly *Cissilopha*). Contrary to patterns found in the New World jay assemblage as a whole and to theoretical predictions, sociality and maturation rates are uncorrelated within the blue-and-black jays. Such a relationship is also lacking in at least one of the other two New World jay lineages that exhibit delayed soft-part color maturation. These results suggest that maturation rates do not track sociality closely and that the occurrence of delayed maturation of soft-part coloration in some New World jay taxa may best be accounted for by phylogenetic inertia. *Received 9 May 1990, accepted 10 Sept. 1990.*

Changes in developmental rates (heterochronic changes) in certain characters leading to retention of "juvenile" characters into later ages may be important in permitting group-living in animals (Hardy 1961, 1974; Brown 1963; Lorenz 1971; Lawton and Lawton 1985). Characters that may serve such a function in certain groups include plumage coloration, absence of male ornamentation, iris color, and beak color. Although several actual mechanisms have been proposed (Hardy 1961, Lawton and Lawton 1985), all share the basic idea that the juvenile character allows greater integration of groups with less aggression. Experimental behavioral studies support these ideas. Hardy (1974) demonstrated experimentally that Beechey's Jays (*Cyanocorax beecheii*) displaying the juvenile (yellow) beak coloration are subjected to less aggression from adults than those with the adult (black) beak color. Lawton et al. (in prep.) demonstrated that the juvenile yellow beak coloration in nestling Brown Jays (*C. morio*) increases food provisioning by adults. Thus, experimental evidence supports the hypothesis that juvenile appearance is an important factor in integrating avian social groups.

Hardy (1961) and Lawton and Lawton (1985) predicted a close relationship between degree of sociality and rates of maturation of characters such as beak color, iris color, and plumage coloration. The present study tests this prediction in the "blue-and-black" jays (formerly *Cissilopha,* now part of *Cyanocorax*) of México and Central America by comparing data on breeding group size with maturation rates of several character sets. This study differs from previous investigations in two regards: (1)

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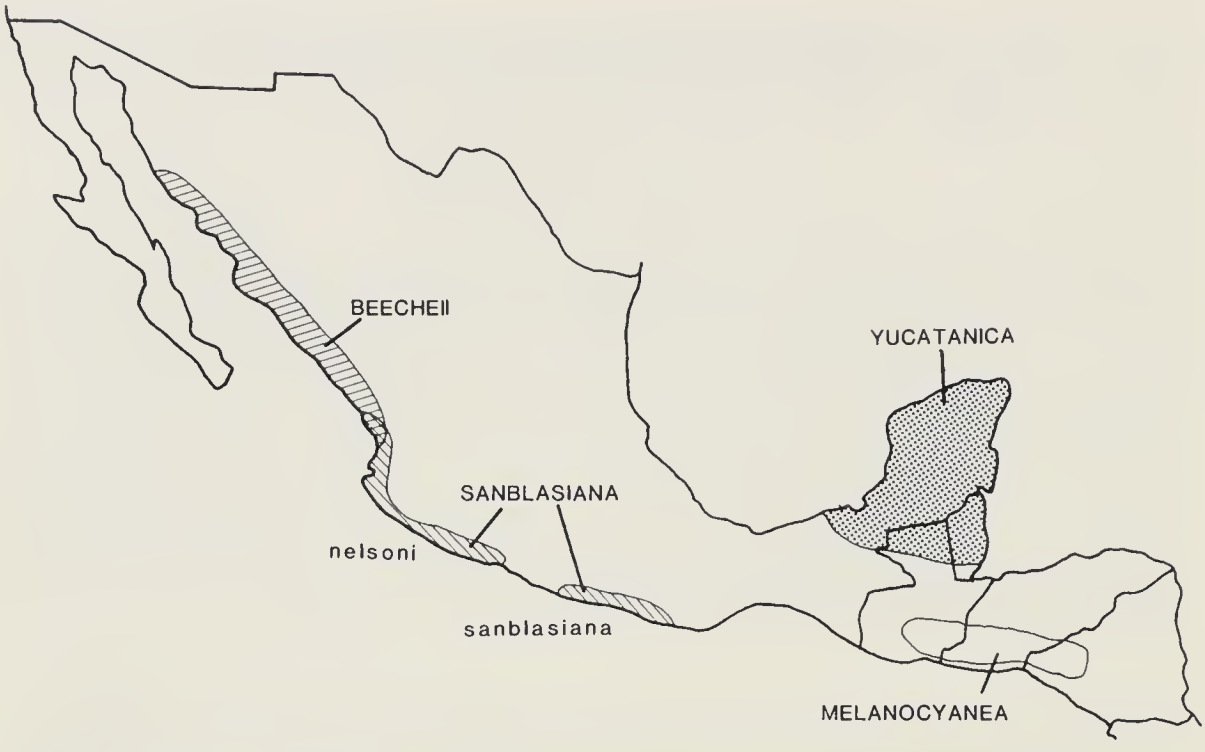

FIG. 1. Geographic distribution of the blue-and-black jays in México and Central America.

comparisons are made within one relatively small lineage instead of across the whole family and (2) singular and plural breeding cooperative breeding systems (Brown 1987) are distinguished in discussing the patterns encountered.

The group under study consists of five largely allopatric populations of four species (Hardy and Raitt 1977; Fig. 1). Some of these populations are highly social, living in large groups that include two or more breeding pairs (plural breeders, e.g., *C. s. sanblasiana,* Hardy et al. 1981), while others live in smaller groups consisting of one pair and occasional helpers (singular breeders, e.g., *C. beecheii,* Raitt and Hardy 1979). Moreover, some populations attain the "adult" black beak coloration at the age of one year or less, while others do not exhibit the black beak color until two or more years of age. Several other characters, such as iris color, tail and body plumage color, and presence of a crest also vary in maturation rate among populations. Thus, the group exhibits marked variation in both degree of sociality and rates of maturation of several morphological characters and is ideally suited to the test.

METHODS

Information on social behavior of the blue-and-black jays was obtained from the literature (Hardy 1976; Raitt and Hardy 1976, 1979; Hardy et al. 1981; Raitt et al. 1984). Data on maturation rates of beak color, iris and circumorbital skin color, presence of a crest, and

tail and body coloration were obtained from Davis (1960), Hardy (1973), and Hardy and Raitt (1977). Because information is not available for each character set in each population of interest, and because Hardy's (1973) studies were based on captive individuals whose ontogenetic trajectories may not be representative of those of wild populations, I reviewed numerous museum specimens from each population. Because the two allopatric subspecies of *C. sanblasianus* differ markedly in social behavior (Hardy et al. 1981), they are treated separately throughout this paper. However, contrary to Hardy and Raitt (1977), it appears that delayed beak color maturation does occur in *C. s. sanblasianus*, given that the only two first-year individuals of this form examined had mandibles more than 50% yellow (Museum of Comparative Zoology 163812, 163813).

I studied 412 (39 *C. beecheii*, 157 *C. melanocyaneus*, 19 *C. sanblasianus sanblasianus*, 89 *C. s. nelsoni*, and 108 *C. yucatanicus*) specimens of blue-and-black jays in the collections of the American Museum of Natural History; Field Museum of Natural History; Museum of Comparative Zoology; Peabody Museum of Natural History; Museo de Zoologia of the Facultad de Ciencias and Colección Ornitológica of the Instituto de Biología, both at the Universidad Nacional Autónoma de México; and the Colección Ornitológica, Universidad Michoacana San Nicolas de Hidalgo. For each specimen, I determined the age as juvenile (0–3 months; having the soft juvenal plumage), first-year (3–15 months; adult coloration, but retaining the primary coverts and rectrices from the juvenal plumage), or after first-year (>15 months, AFY), using molt-sequence descriptions in Pitelka (1945). Additional categories could not be created for lack of information on molt schedules in each population.

I estimated the percent of mandible surface area that was yellow to the nearest 5% by visually dividing the mandible surface into four sections, scoring each as yellow, partly yellow, or black and combining these scores into an overall estimate. Because coloration patterns of the maxilla and mandible are highly correlated (Pearson's product-moment correlation, $r = 0.948$, N = 412), and for the sake of simplicity, I analyze here only data on mandible coloration.

Sexual differences in maturation rates are not evident (see Selander 1959). In the one case in which sample sizes and the pattern of variation permitted statistical testing, beak color maturation rates did not differ between the sexes (*C. melanocyaneus*, first-year, contingency test dividing above and below 50% yellow, $\chi^2 = 0.417$, df = 1, $P = 0.52$). Hence, sexes are combined in the analyses that follow.

RESULTS

Beak color maturation curves (Fig. 2) vary significantly (comparing mandible coloration in first-year individuals, Kruskal-Wallis Test, KW = 62.6, df = 3, $P < 0.001$) among the five populations of blue-and-black jays. The most rapid maturation of beak color occurs in *C. s. nelsoni*, *C. s. sanblasianus*, and *C. melanocyaneus* in which juveniles have nearly completely yellow beaks, but these darken rapidly, so that nearly all after first-year (AFY) individuals have completely black beaks (Fig. 2). Based on a very small sample, *C. beecheii* appears to mature more slowly. *C. yucatanicus* matures significantly slower than the other populations (Kruskal-Wallis test with multiple comparisons, $H = 63.87$, $P < 0.05$, Siegel and Castellan 1988), having completely yellow beaks until after they reach the AFY stage.

Other characters also show variation in maturation rate among blue-

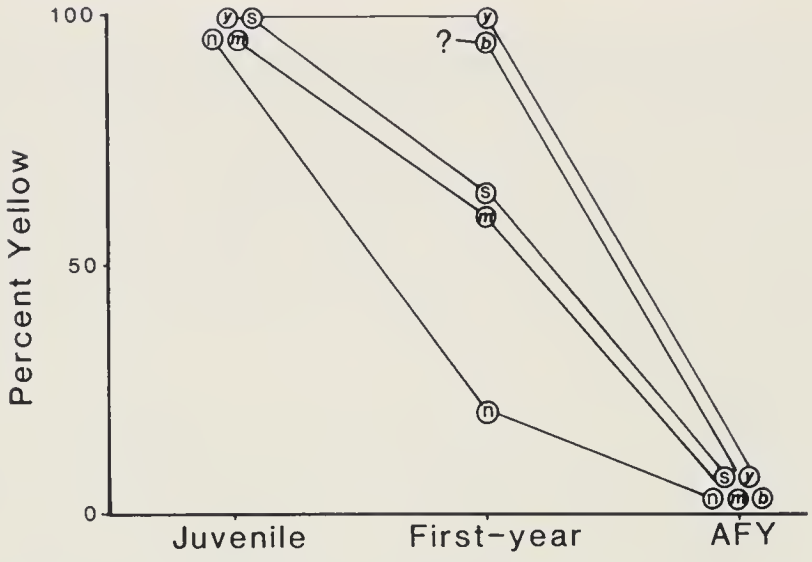

FIG. 2. Maturation rates of beak coloration in five populations of blue-and-black jays shown as the median percent yellow of mandible surface area.

and-black jay populations, including iris color, presence of a crest, and tail and body coloration (Table 1). Maturation times (i.e., age at which adult appearance is attained) vary widely. Maturation times for iris color range between 19.5 and 39 mos (Hardy 1973). The crest requires between three and 27 mos and tail color requires between three and 15 mos. Maturation rates in different characters are not significantly concordant (Kendall Coefficient of Concordance, $W = 0.310$, $P > 0.05$, Siegel and Castellan 1988).

The degree of sociality also varies strongly in the blue-and-black jays (Table 2). Group size and breeding units per group are smallest in *C. beecheii* and *C. s. nelsoni,* intermediate in *C. melanocyaneus* and *C. yucatanicus,* and largest in *C. s. sanblasianus. C. beecheii* and *C. s. nelsoni*

TABLE 1

SUMMARY OF MATURATION RATES (AGE IN MONTHS AT WHICH MOST INDIVIDUALS ARE INDISTINGUISHABLE FROM ADULT) OF SOFT-PART COLORATION IN THE BLUE-AND-BLACK JAYS, BASED ON DATA GATHERED IN THIS STUDY, AND ON HARDY (1973) AND HARDY AND RAITT (1977). "EYE" REFERS TO COLORATION OF THE IRIS AND/OR CIRCUMORBITAL SKIN

Population	Beak	Eye	Crest	Tail
C. beecheii	15	27	3	3
C. melanocyaneus	9	19.5	3	3
C. sanblasianus nelsoni	9	39	27	3
C. s. sanblasianus	9	27	15	3
C. yucatanicus	>15	27	3	15

TABLE 2

SUMMARY OF ASPECTS OF SOCIALITY IN THE BLUE-AND-BLACK JAYS FROM HARDY (1976), RAITT AND HARDY (1976), HARDY ET AL. (1981), AND RAITT ET AL. (1984)[a]

Population	Sample size	Breeding units	Non-breeders	Group size
Cissilopha beecheii	5, 7, 8, 10, 6	1.0	1.8	3.8
C. melanocyaneus	1	1.2[b]	9.0	11.0
C. sanblasianus nelsoni	2	1.0	2.5	4.5
C. s. sanblasianus	2, 2	6.1	7.0	19.0
C. yucatanicus	10, 9	1.2	7.4	11.9

[a] Individuals listed are yearling or older. Sample sizes are number of groups examined per year. Data for particular groups are averaged over years when data from multiple years are available. Number of non-breeders assumes two breeding adults per active nest (i.e., no polygamy).

[b] Sample size six.

have few non-breeding individuals. The three measures of sociality are not independent of one another (Kendall Coefficient of Concordance, $W = 0.816$, $P < 0.05$).

No direct relationship is apparent between the measures of sociality and maturation rates of the various characters. Fig. 3 shows the relationships between maturation rates of the four characters and three measures

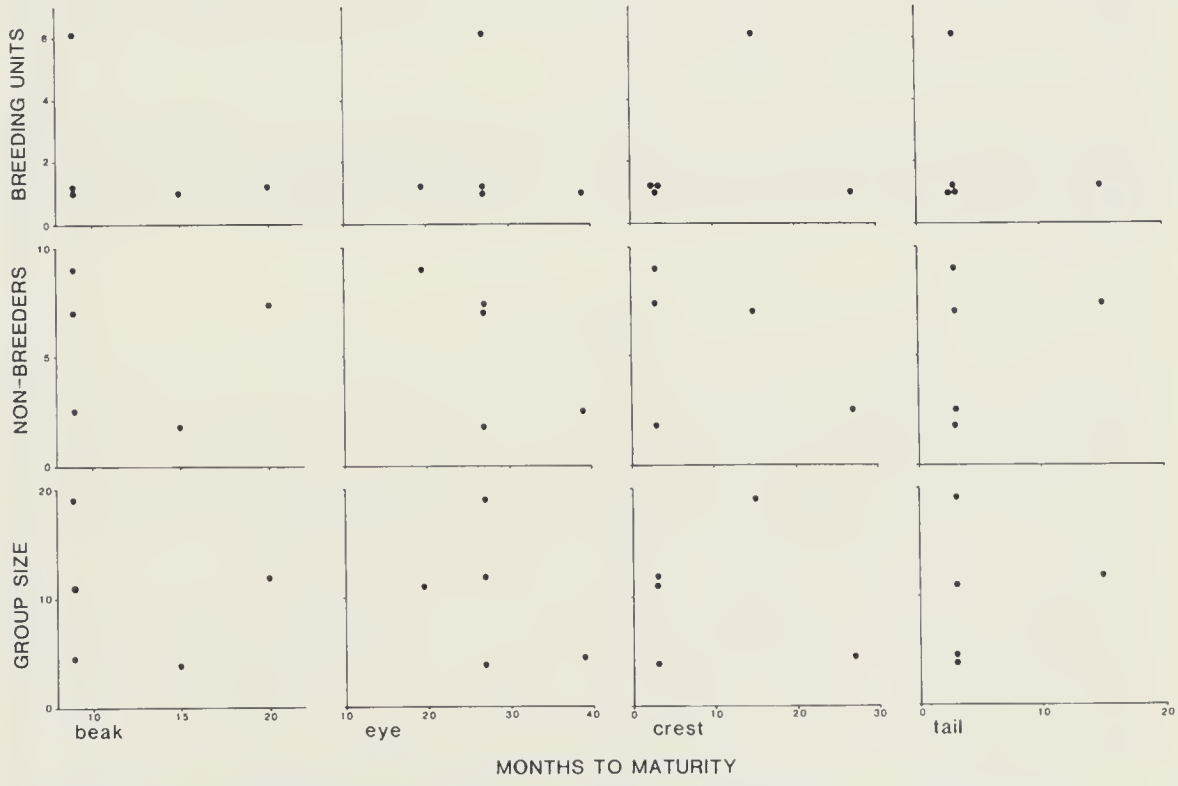

FIG. 3. Relationship between maturation rates of various character sets and degree of sociality in the blue-and-black jays.

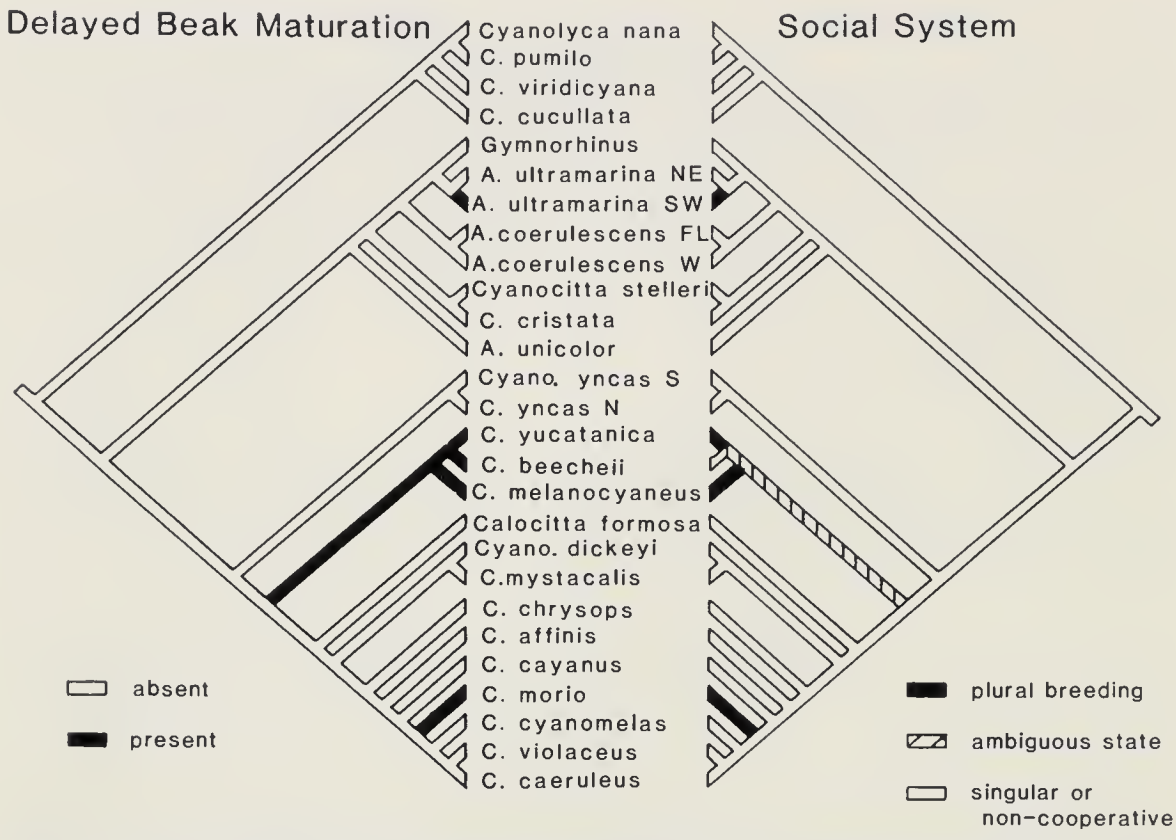

FIG. 4. Relationship between phylogenetic distribution of communal breeding and delayed beak color maturation in the New World jays. (Information on sociality is from Goodwin 1976. The phylogeny is from Hope [1989, Fig. 24b]. Reconstructions of character-state histories were produced using the MACCLADE package [Maddison and Maddison 1987].)

of sociality. None of the twelve Spearman rank-order correlation coefficients between the three measures of sociality and the four characters is significantly different from zero ($P > 0.05$). The coefficients range from -0.224 to 0.707.

DISCUSSION

In the New World jay assemblage as a whole, sociality and delayed maturation of beak color are highly correlated in their occurrence (Hardy 1961, Lawton and Lawton 1985; Fig. 4). Singular cooperative breeding (viz, one pair with helpers, Brown 1987) is widespread in the assemblage and apparently represents the plesiomorphic state (i.e., that present in the most recent common ancestor of the group). The phylogenetic distribution of singular cooperative breeding shows no obvious relation to that of delayed beak color maturation. Plural breeding (viz, more than one breeding unit per group, Brown 1987), however, is rarer in the New World jays, probably having been derived three or four times independently (Fig. 4). Interestingly, delayed beak color maturation exists only in these same lineages. The Unicolored Jay (*Aphelocoma unicolor*) is not considered to

show delayed maturation, as the delay in its beak color maturation appears to be minor (Peterson, unpubl. data). Thus, the prediction of a correlation between maturation rates of soft-part coloration and a high degree of sociality is strongly supported in the assemblage as a whole.

Why might there be a relationship between *plural* breeding and delayed soft-part maturation? Other workers who have treated these problems have either not considered the differences between singular and plural breeding (Lawton and Lawton 1985) or have assumed that individuals with "juvenile" characters were non-breeders (Hardy 1961). It is possible, however, that juvenile-like appearance may facilitate plural breeding by making it easier for a young bird to attempt early breeding inside the natal territory (R. Curry, pers. comm.). Under this view, delayed soft-part color maturation in plural breeders may act in the manner suggested for other songbirds (Rohwer 1978, Rohwer et al. 1980).

Within the New World jay assemblage, three lineages show delayed soft-part color maturation. This study focuses on variation in sociality and maturation rates within one of these lineages and finds no relationship.

In the Mexican Jay (*A. ultramarina*), a second New World jay lineage showing delayed color maturation, close correspondence between sociality and ontogenetic patterns similarly is lacking (Brown and Horvath 1989, Peterson, unpubl. data). The two populations in the United States suggest such a correlation, as Arizona and New Mexico populations breed plurally in large social groups and show delayed beak color maturation, while Texas populations are found in smaller groups (Ligon and Husar 1974, Strahl and Brown 1987, Brown and Horvath 1989) and do not exhibit delayed maturation (Pitelka 1951). However, the relationship breaks down farther south in eastern México, where social groups are large, yet color maturation is not delayed (Brown and Horvath 1989, Peterson unpubl. data).

For the third lineage showing delayed color maturation (*C. morio*), critical data on geographic variation in social-group size are lacking. Lawton and Lawton (1985) predicted that populations at the northern edge of the species' range in Texas and the state of Tamaulipas in México would be less social and show more rapid beak color maturation. However, comparing first-year individuals from Tamaulipas with similar-aged individuals from Costa Rica and Panama in the collections of the Field Museum of Natural History, I found that the northern populations actually mature significantly more slowly than those from the south (comparing percent yellow on mandible in first-year individuals, Mann-Whitney U-test, $U = 34$, $P \leq 0.005$, N = 5, 7). Clearly, more data on geographic variation in social-group size are needed before any predictions can be tested in this species.

Hence, in spite of a strong correlation between delayed maturation and plural breeding across the New World jay assemblage, and contrary to theoretical predictions, no such relationship exists *within* at least two of the three lineages exhibiting delayed color maturation. One potential explanation is that although delayed maturation may be an important factor in the evolution of avian plural breeding, its presence in less complex social systems may not be selected against. If the ancestral blue-and-black jay or *A. ultramarina* bred plurally, and the lower degree of sociality in some populations (e.g., *C. beecheii, A. u. couchii*) represents an evolutionary reversal, these populations may exhibit delayed soft-part color maturation as a result of phylogenetic inertia.

Thus, in spite of a close correlation in the New World jay assemblage as a whole, the current diversity of soft-part color maturation rates in the blue-and-black jays is not closely related to the degree of sociality. However, the adaptive hypothesis regarding sociality and maturation rates discussed in the introduction is not necessarily refuted. Delayed maturation rates may have been an important factor in the evolution of extreme sociality in the jays, but have not disappeared in lineages showing secondary reductions in levels of sociality.

ACKNOWLEDGMENTS

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CHARACTERIZATION OF GRIT USE BY CORNFIELD BIRDS

Louis B. Best and James P. Gionfriddo[1]

Abstract.—Grit use (frequency, amount, size, shape, and roundness) was characterized for 22 bird species that commonly use midwestern cornfields during the breeding season. The frequencies of occurrence and the median amounts of grit found in birds' gizzards differed greatly among the species, ranging 15–100% and 0–69, respectively. The grit-size distribution profiles of most species had definite peaks, with grit use declining abruptly on either side of the preferred grit size. In general, grit size increased linearly with the $\log_{(10)}$ of body mass. Grit particles ranged in shape from spherical to oblong; species more specialized in their selection of grit shapes tended to use spherical or nearly spherical grit. Most grit found in gizzards was intermediate between having sharp, irregular surfaces and having smooth, rounded surfaces. Overlap in the characteristics of grit used by birds and the characteristics of granular insecticides can be used to evaluate the likelihood that birds will pick up insecticide granules as a source of grit. *Received 26 April 1990, accepted 25 Sept. 1990.*

Granular insecticides are used extensively for pest control, especially in the Midwest, where millions of acres of corn are treated each year to control corn rootworms, cutworms, and corn borers (U.S. Dept. Agric. 1985). All major granular insecticides used for this purpose are highly toxic to birds (Schafer et al. 1983), and there have been numerous reports of avian mortality associated with granular insecticide use (e.g., see U.S. Environ. Protect. Agency 1989). Thus, treated fields constitute a potential avian hazard. Birds foraging in cornfields may inadvertently or intentionally pick up these granules; the latter probably occurs when birds mistake the granules for grit or, less likely, food. Very little is known about the grit use of birds that commonly frequent cornfields; the best documentation of grit use is for gallinaceous species, but that focuses on the birds' needs for calcium during egg-shell formation (Sadler 1961, Harper 1964, Korschgen 1964). An understanding of avian grit-use patterns is needed to assess potential avian risks to granular insecticides. If the characteristics of grit naturally selected by the birds are known, then those characteristics can be compared to the characteristics of various insecticide granules to determine the degree of similarity, and thus, the potential for birds to mistake granules for natural grit. In this report, we systematically characterize the grit-use patterns of 22 bird species that commonly use midwestern cornfields during the breeding season. We

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collected over 16,400 grit particles obtained from 770 individual birds. Our hope is that such information will ultimately be used to reduce avian risks where granular insecticides are applied.

METHODS

Grit use was characterized for 22 bird species known to use cornfields during the late spring and summer (Best et al. 1990), the period when granular insecticides are applied to control corn pests. (See Appendix I for the list of species and their scientific names.) The species included all those that exclusively (two species) or regularly (seven species) use cornfields during the breeding season and many of the species that are occasional visitors to cornfields. In addition, the two major upland gamebirds in the Midwest (Ring-necked Pheasant and Northern Bobwhite) were included.

The birds were obtained opportunistically from a variety of sources that included roadkills, birds collected specifically for this or other research projects, and hunter-harvested birds. At least 20 individuals of each species were collected. Most birds were secured during the spring and summer; exceptions were the Northern Bobwhite (collected primarily in December and January), Ring-necked Pheasant (October–December), and American Crow (December and February). In general, birds were obtained from Iowa or other midwestern states, although most of the Horned Larks were collected in Utah.

The gizzards were removed from all collected birds, labeled, and preserved in 75% ethanol until their contents could be examined in the laboratory. In the laboratory, each gizzard was sliced in half with a razor blade and its contents flushed into a petri dish. The gizzard contents were then examined and systematically sorted under a zoom, stereo microscope. All grit particles encountered were separated from the remainder of the gizzard contents. The search for grit particles was considered complete when a complete scan of the petri dish contents resulted in no additional grit particles being found. (Particles <0.1 mm in size were excluded because they were considered soil material and not grit selected by the birds.)

The number of grit particles found in each gizzard was counted, and the particles were characterized on the basis of their size, shape, and roundness. The longest and shortest dimensions of each grit particle were measured to the nearest 0.01 mm with a digital caliper (Mitutoyo model 500 digimatic), and these two values were then averaged for an overall measure of grit size. A grit-shape index value was calculated for each grit particle by dividing the longest dimension by the shortest dimension. These values were ≥ 1.0, with 1.0 representing a spherical shape and larger values representing oval to oblong shapes. Grit roundness, a variable used to characterize the grit surface, was classified into five categories using a scheme developed by petrologists to describe mineral grains (El-Hinnawi 1966:15) (Fig. 1).

Gizzards completely devoid of food were not included in the data presented here because of the potential that they represented abnormal conditions. Furthermore, gizzards containing appreciable amounts of soil (i.e., hundreds of grit particles <0.2 mm in size) were excluded because they likely resulted from conditions where soil had been ingested inadvertently with the food (e.g., soil adhering to food surfaces) rather than being intentionally picked up by birds as grit. Less than 2% of the gizzards collected were discarded for the latter reason.

RESULTS

Frequency and quantity of grit use.—The 22 bird species studied differed both in the amounts of grit present in their gizzards and in the proportions of their gizzards containing grit (Fig. 2). The frequencies of occurrence of grit in gizzards of Dickcissels (15%, N = 20), Eastern Kingbirds (19%, N

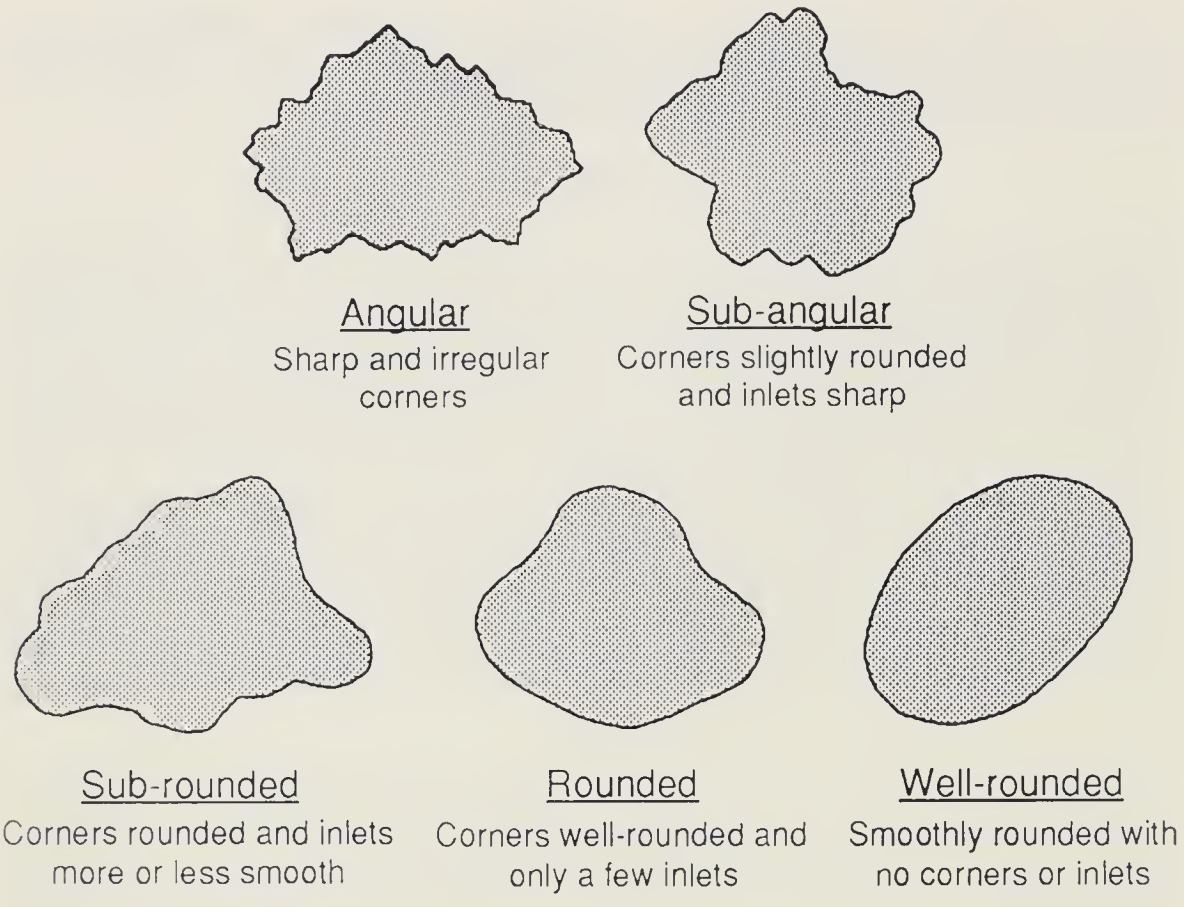


FIG. 1. Five categories used to characterize grit roundness.

= 26), and Barn Swallows (22%, N = 23) were particularly low, and less than 30 grit particles were obtained from each of these species. In addition, less than half of the gizzards of European Starlings, Red-headed Woodpeckers, and American Robins contained grit. The low occurrence of grit in Barn Swallows and Eastern Kingbirds was expected, in that these species are aerially feeding insectivores (De Graaf et al. 1985), and there is evidence that insectivorous birds often use less grit than birds with other diets (Alonso 1985; Best and Gionfriddo, unpubl. data). In contrast, the relatively infrequent grit use by Dickcissels and European Starlings was surprising because these birds are ground-foraging omnivores, as are most of the other species studied. The frequency of occurrence of grit in gizzards of several species was relatively high (Fig. 2), notably the Ring-necked Pheasant, Savannah Sparrow, House Sparrow, and Horned Lark.

The amount of grit found in the birds' gizzards differed greatly (Fig. 2). House Sparrow and Ring-necked Pheasant gizzards generally had the greatest amounts of grit; median grit counts in Savannah Sparrow, Blue Jay, and Northern Bobwhite gizzards also were relatively high. (The largest grit count documented for a single gizzard was of a female Ring-necked Pheasant in April, at the beginning of the nesting season.) As expected,

the species with the lowest proportions of gizzards with grit also had the lowest grit counts per gizzard. Median grit counts per gizzard for the Dickcissel, Eastern Kingbird, and Barn Swallow were all 0 (the ranges were 0–2, 0–1, and 0–21, respectively). When all species were compared simultaneously, an exponential relationship was found between the median number of grit particles per gizzard and the proportion of gizzards containing grit (Fig. 3). The amount of grit in the gizzards of most species was highly variable (Fig. 2). For example, median grit counts for Red-headed Woodpeckers, American Crows, and American Robins were all two or less, yet individual grit counts per gizzard ranged to over 100.

Grit size.—Mean grit size was related to bird body size (Fig. 4); grit size increased linearly with the $\log_{(10)}$ of the body mass. (Grit size, shape, and roundness data are not presented for species from which fewer than 50 grit particles were collected.) The linear regression line derived from the data described the relationship between grit size and body size well for most species. Exceptions were the American Crow, which used larger grit than expected based on its body size, and the Common Grackle, Red-headed Woodpecker, and American Robin, which used unusually small grit for their body masses. We cannot explain why the grit-size preferences of these species differed from the others. The crow and grackle are ground-foraging omnivores; the robin also forages primarily on the ground, although it sometimes feeds in the canopies of trees and shrubs; and the Red-headed Woodpecker feeds primarily on insects, either on trees or in the air (De Graaf et al. 1985). Perhaps some of the small grit in the robins' gizzards was not actually selected by the birds as grit, but rather was eaten incidentally when they ingested earthworms. (These particles could have been inside the earthworms' guts or adhering to the surface of the worms.) Earthworms are the primary food of robins during spring and early summer (Walton 1928, Johnson et al. 1976).

The distributions of grit sizes used by the various species differed greatly (Fig. 2). Several species (Red-headed Woodpecker, American Robin, House Sparrow, Common Grackle, Brown-headed Cowbird, Indigo Bunting, and Savannah Sparrow) were relatively restricted in their selection of grit sizes. This was evaluated by determining the minimum number of 0.2-mm size classes needed to comprise 80% of the grit particles sampled for each species. The Ring-necked Pheasant and American Crow used the broadest ranges of grit sizes of the 19 species evaluated. The breadth of grit sizes used, however, was related linearly to the mean grit size; birds that generally used larger grit also were more variable in their selection of grit size (Fig. 5). Considering this, European Starlings were particularly variable in their choices of grit sizes when compared with other species whose average grit sizes were similar. Conversely, although the American

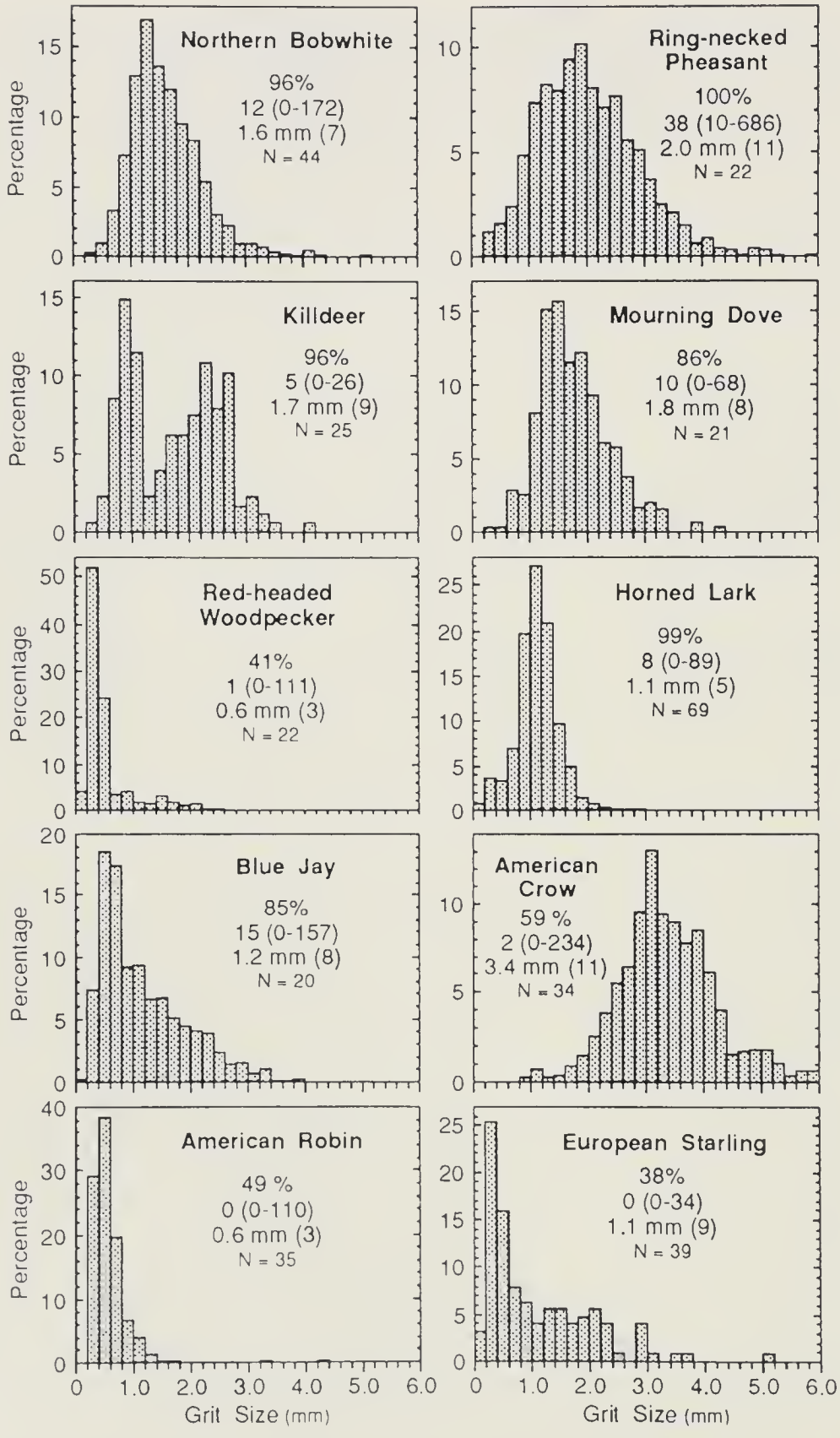
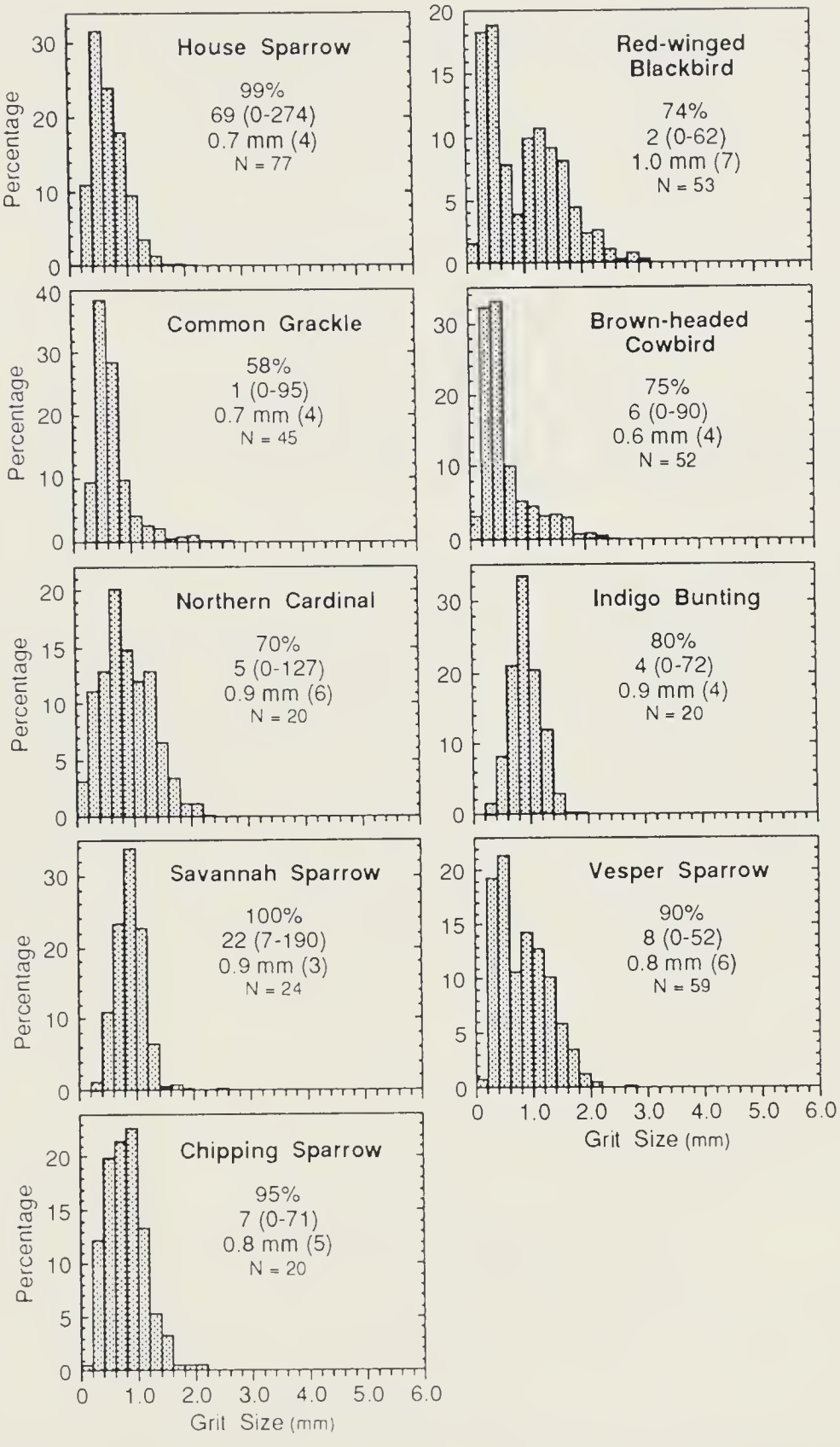


FIG. 2. Size distributions of grit particles found in cornfield bird gizzards. Also given are the proportion (%) of gizzards in which grit particles were found, the median (range) number of grit particles found per gizzard, the mean grit particle size, the number of 0.2-



mm size classes comprising 80% of the grit particles sampled (in parentheses), and the number of birds sampled.

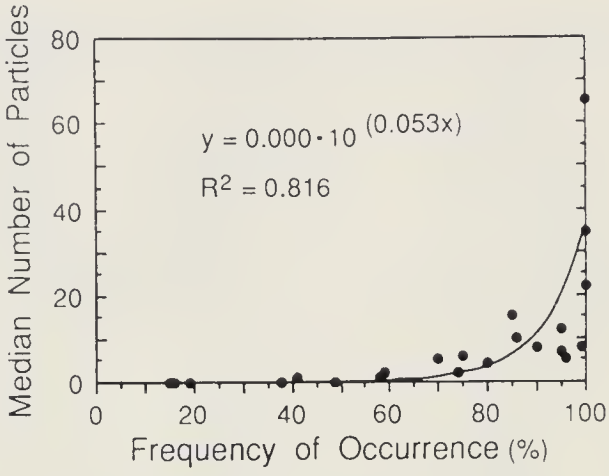


FIG. 3. Relationship between the median number of grit particles per bird and the proportion (%) of birds with grit. Each dot represents a species.

Crow selected, on average, the largest grit, its variation in grit-size use was less than expected based on the pattern of the other species.

The grit-size distribution profiles of most species had definite peaks, with grit use declining noticeably on either side of the preferred grit size (Fig. 2). Typically, the decline was more abrupt on the lower end of the size range than on the upper. The grit-size distributions of the Killdeer and Red-winged Blackbird are noteworthy because they did not exhibit a single grit-size preference; both seemed to have two preferred grit sizes. The bimodal distribution of grit sizes found in Killdeer and redwing gizzards was not related to differences in grit use between males and females (Killdeer mean grit size: males = 1.9 mm, females = 1.7 mm, *t*-test, $P > 0.1$; Red-winged Blackbird: males = 1.1 mm, females = 1.2

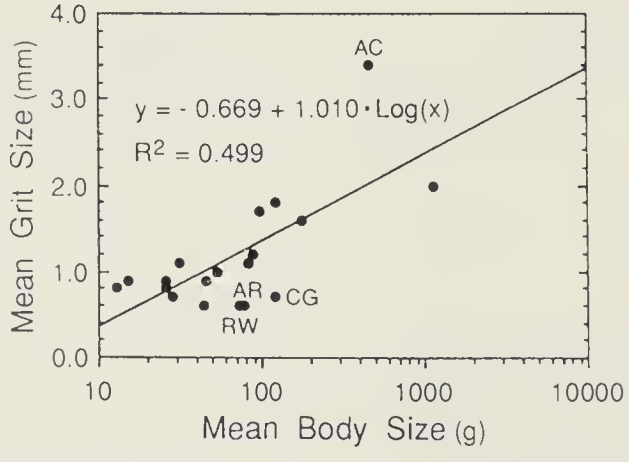


FIG. 4. Relationship between mean grit size and mean bird body mass. Body masses were obtained from Dunning (1984); for sexually dimorphic species, male and female body masses were weighted equally in determining means. Each dot represents a species; species for which fewer than 50 grit particles were collected are not included.

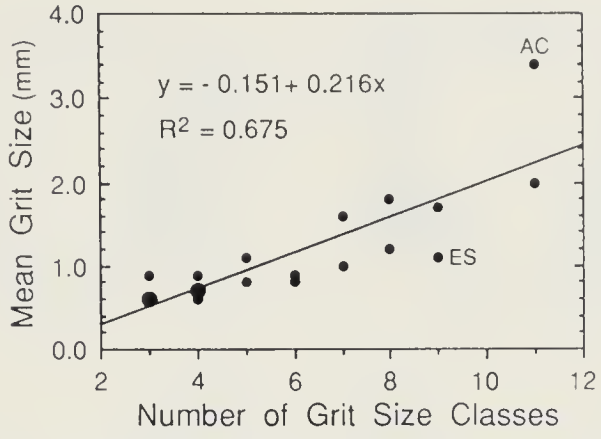


FIG. 5. Relationship between mean grit size and the number of 0.2-mm size classes comprising 80% of the grit particles sampled. Each small dot represents a species; the large dots each represent two species. Species for which fewer than 50 grit particles were collected are not included.

mm, $P > 0.1$) and did not seem to be related to other factors (e.g., month when the bird was collected). The grit-use pattern of these two species may be a sampling artifact, although the distinctness of the two peaks (particularly for the Killdeer) and the numbers of birds sampled argue against this supposition.

The amount of grit in the gizzards of some species seemed to be related to the size of grit. When this occurred, gizzards with more grit tended to have smaller-sized grit particles. This pattern was most evident in Brown-headed Cowbirds, but it also seemed to occur in other species (e.g., Blue Jays and Red-winged Blackbirds). For cowbirds, when the mean size of grit in gizzards was ≤ 0.7 mm, the average number of grit particles was 29.8; but when the mean size was >0.7 mm, the average number of grit particles was 8.4 ($t = 3.22$, 37 df, $P < 0.01$). Similar measures for the Blue Jay were mean grit size ≤ 1.0 mm, mean grit count 72.0; mean grit size > 1.0 mm, mean count 28.4. For the Red-winged Blackbird the values were: mean grit size ≤ 1.0 mm, mean grit count 14.1; mean grit size > 1.0 mm, mean count 7.4. Neither of the differences for the latter two species, however, were statistically significant (t-test, $P > 0.1$).

Grit shape.—Grit particles can range in shape from nearly spherical (shape index approaching 1.0) to oblong, in which the longest dimension may exceed the shortest by several times (Fig. 6). The grit shapes selected by the 19 cornfield birds differed considerably. The American Crow showed the strongest tendency to use spherical grit; almost 40% of the grit found in gizzards of this species had a shape index of less than 1.2. Grit used by Red-headed Woodpeckers and American Robins also tended to be spherical or nearly spherical. The grit particles most frequently used by

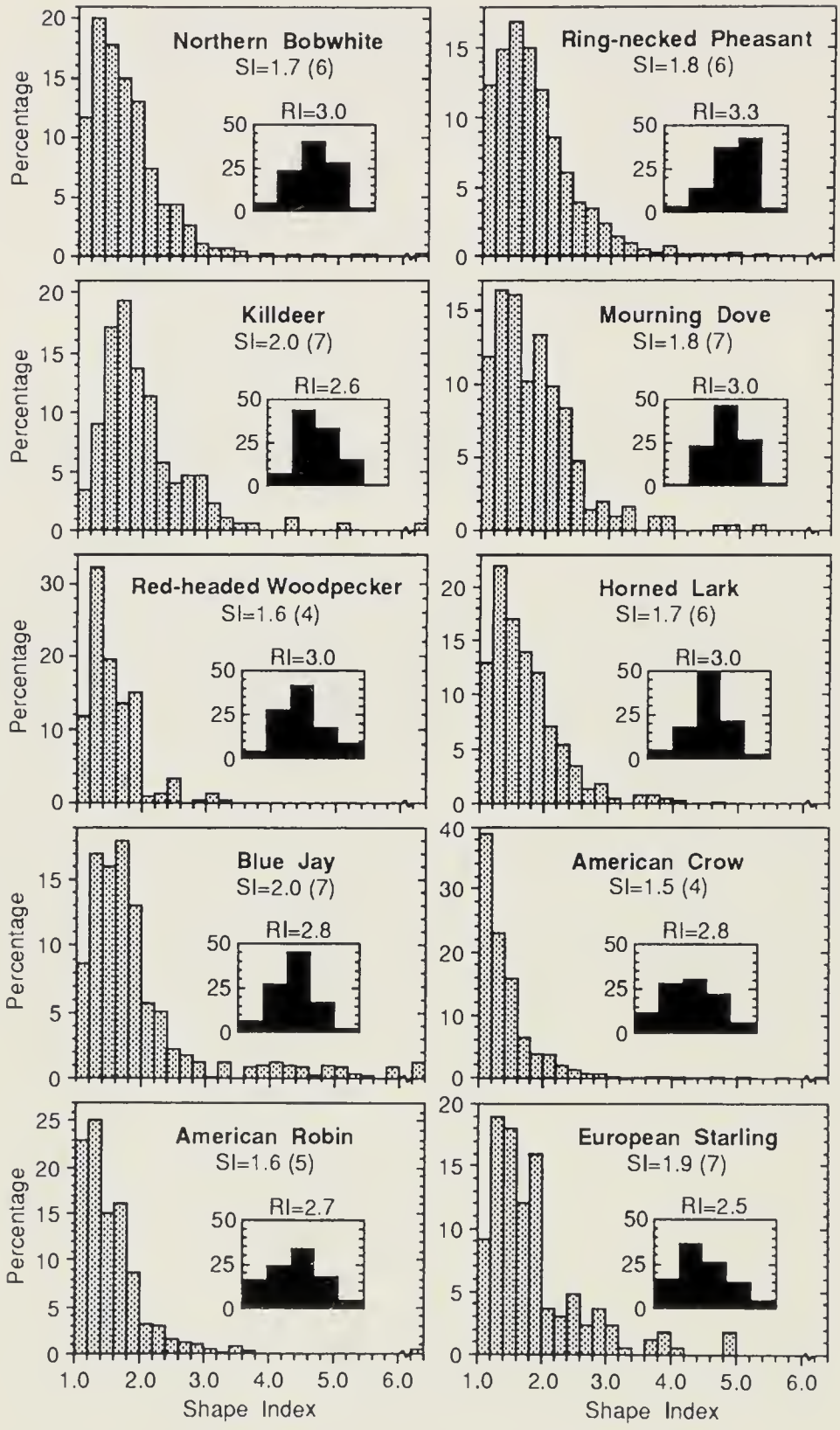
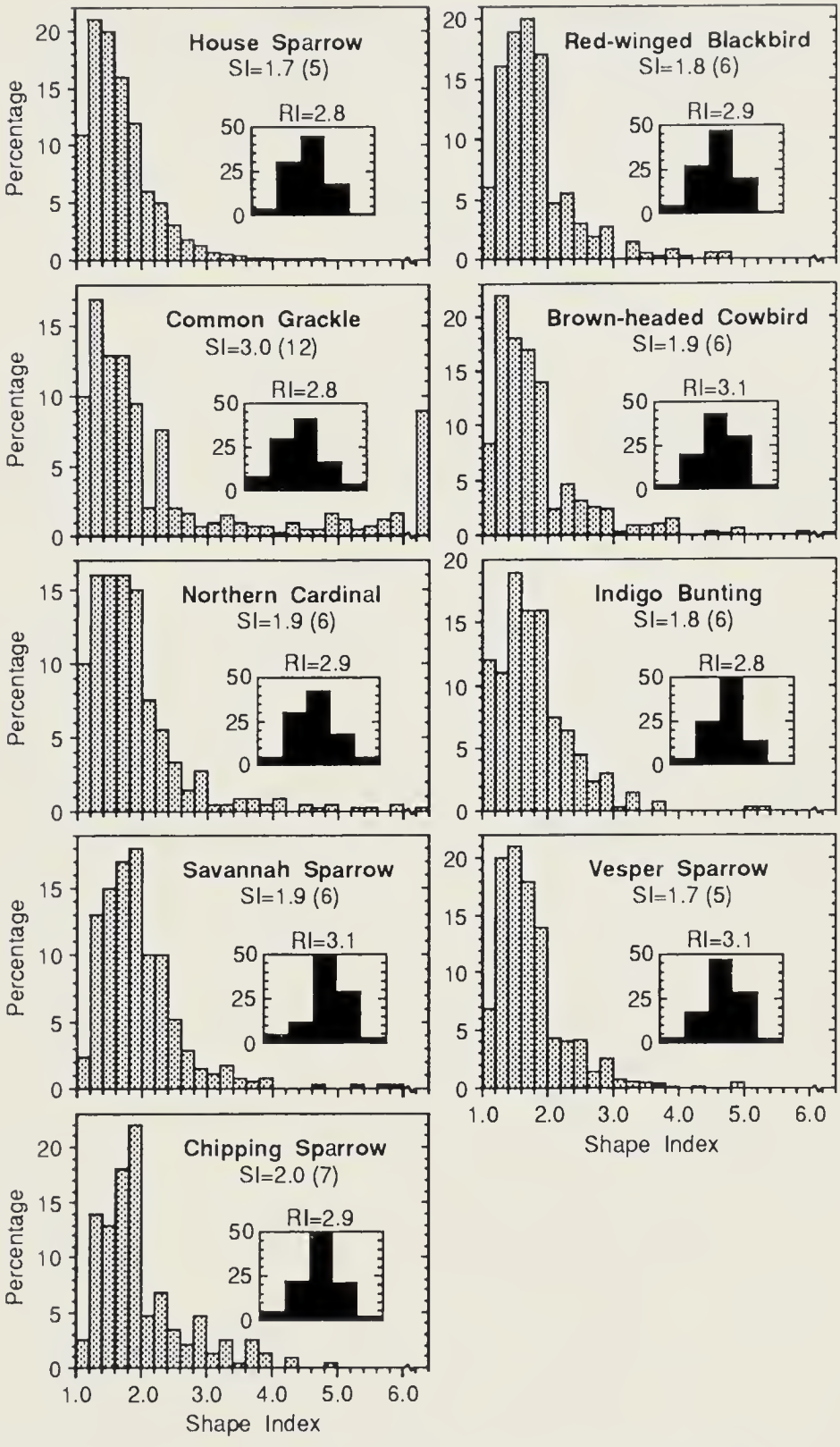


FIG. 6. Distribution of grit particles found in cornfield bird gizzards among the shape-index classes (stippled histogram) and among the roundness categories (black histogram). The last shape category represents grit particles with index values >6.0. The five roundness categories are (left to right): angular, sub-angular, sub-rounded, rounded, and well-rounded.



The SI (shape index) is the overall mean shape-index value, and the value in parentheses is the number of shape classes comprising 80% of the grit particles sampled. The RI (roundness index) is an overall mean roundness value computed by giving grit particles in the angular category a value of 1, those in the sub-angular category a value of 2, etc.

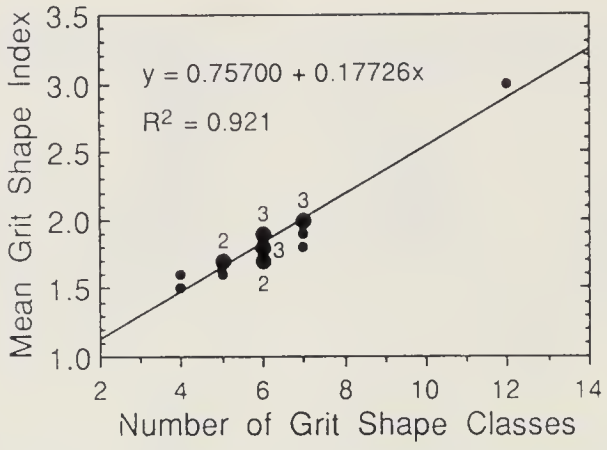


FIG. 7. Relationship between the mean grit shape-index value and the number of grit shape classes comprising 80% of the grit particles sampled. Each dot represents a species unless indicated otherwise. Species for which fewer than 50 grit particles were collected are not included.

other species (e.g., Killdeers, Blue Jays, Common Grackles, and Chipping Sparrows) tended to be more oblong.

The variability of grit shapes found in gizzards also differed among the 19 bird species sampled (Fig. 6). As with grit size, variation in grit shape was determined by counting the minimum number of grit-shape index classes needed to comprise 80% of the grit particles sampled for each species. The American Crow and Red-headed Woodpecker exhibited the most restricted use of grit shapes. American Robins, House Sparrows, and Vesper Sparrows also were relatively specialized in their choices of grit shapes. In contrast, the Common Grackle, and to a lesser degree the Blue Jay, tended to use wide ranges of grit shapes. Nine percent of the grit particles found in grackle gizzards had shape index values >6.0, and 12 shape classes were needed to comprise 80% of the grit sampled for this species. When all species were compared, a general pattern became evident (Fig. 7). Species specializing in their selection of grit shapes tended to use spherical or nearly spherical grit, whereas species using disproportionately more oblong grit tended to be more generalized in their choice of grit shapes.

Grit roundness.—Grit particles ranged from having surfaces with sharp and irregular "corners" (i.e., projections) to having surfaces that were very round and devoid of irregularities (Figs. 1 and 6). In general, most grit particles found in gizzards had intermediate surface characteristics, that is, most were classified as sub-angular, sub-rounded, or rounded. Very few particles were categorized as well-rounded. Of the bird species studied, the Killdeer, American Robin, and European Starling had the highest proportions of angular-shaped (angular and sub-angular) grit in their giz-

zards. This was particularly true for starlings and Killdeers, whose gizzards contained over 50% angular and sub-angular grit. Ring-necked Pheasants, Brown-headed Cowbirds, Savannah Sparrows, and Vesper Sparrows generally used more rounded, smooth-surfaced grit than did the other species, but even in these species, very few grit particles were classified as well-rounded.

DISCUSSION

Comparisons across species revealed no consistent relationships between grit use with respect to one grit characteristic and grit use relative to other characteristics. This was true both for comparisons of overall mean values and for comparisons of the ranges of values chosen. That is, mean grit size was not related to mean grit shape, range in grit size was not related to range in grit shape, etc. Some individual species, however, did show certain noteworthy patterns. For example, although the American Robin and Red-headed Woodpecker had comparatively low proportions of gizzards containing grit (<50%), they were very restrictive in their choice of grit size and shape, seeming to prefer small, spherical grit (Figs. 2 and 6). These species also used relatively small grit for their body size (Fig. 4). The House Sparrow also used restricted ranges of grit sizes and shapes, but in contrast to the robin and Red-headed Woodpecker, grit was almost always present in gizzards of this species. The Common Grackle and American Crow represented some interesting contrasts in grit use. The grackle was relatively restricted in its choice of grit size, selecting grit comparatively small for its body size. Yet this species showed little apparent selectivity for grit shape. The crow demonstrated exactly the opposite pattern; it used a broad range of grit sizes comparatively large for its body size, yet chose a very restricted range of grit shapes.

Grit use by birds is influenced by grit availability; thus, grit-use patterns do not necessarily reflect grit preferences. This is probably least likely a concern relative to the amounts and sizes of grit consumed because these birds were collected primarily during the summer when snow and ice cover would not have restricted bird access to the soil surface. Furthermore, most birds came from the Midwest, where the land is used mainly for agricultural production, resulting in a relatively large proportion of exposed soil, and where gravel-surfaced secondary roads surround almost every section. The availability of grit of various shapes and, in particular, the availability of grit representing various degrees of roundness are determined largely by the sources of the grit and the history of exposure of the grit to erosion. The relatively low frequencies of occurrence in gizzards of grit in the well-rounded and angular classes (Fig. 6) could be attributed

to limited availability of these forms of grit. It would be useful to sample the shape and roundness of grit available to birds in their natural environment to assess preferences. The most precise tests of grit choice, however, would require birds to be studied in captivity where grit access could be controlled. We currently have such research under way to further evaluate grit preferences in House Sparrows.

Our characterization of the grit found in birds' gizzards represents a "snapshot" appraisal of grit use. In reality, grit selection and use is a dynamic process—grit is consumed, retained in the gizzard for a finite period of time, and then voided from the gastrointestinal tract. How long grit remains in the gizzards of birds and the degree to which grit size, shape, and roundness influence grit retention are largely unknown. The grit found in birds' gizzards depends not only upon grit selection (i.e., preference and availability) by the birds but also on the mechanisms of grit retention. Grit selection determines the range of grit that can potentially be present in gizzards, but the grit retention process determines which grit particles are retained in the gizzard and for how long. Research is needed to differentiate between the grit selection and grit retention processes.

The amounts and types of grit consumed by birds are determined not only by availability (see above), but also by other factors such as diet (e.g., Norris et al. 1975, Alonso 1985) and stage in the reproductive cycle (e.g., Harper 1964, Kopischke 1966). These factors often differ among seasons or geographical locations; thus, data collected in one study may not be representative of conditions elsewhere. Our study was designed to characterize grit use by birds frequenting midwestern cornfields in spring and summer. Grit-use patterns documented under other circumstances may or may not be similar to those we report. Our study is, however, the first attempt of its kind, and thus provides important baseline data that can serve as a basis for comparison with other research findings.

Grit preferences of birds should be considered when evaluating avian risks from granular insecticides. The amount of overlap between the size, shape, and roundness of granular insecticides and the size, shape, and roundness of grit naturally selected by individual bird species can be used to evaluate the likelihood that the birds will pick up the granules as a source of grit. Where the overlap is greater, the probability that the birds will consume the granules will be greater. This would be particularly true for those species that have relatively restricted preferences for grit size, shape, or roundness. The relative importance of these three grit characteristics in determining grit use is birds in unknown but needs to be evaluated, particularly if such information is to be used in designing insecticide granules to make them less attractive to birds.

ACKNOWLEDGMENTS

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Appendix I

Scientific Names of the Bird Species Studied

Common name	Scientific name
Northern Bobwhite	*Colinus virginianus*
Ring-necked Pheasant	*Phasianus colchicus*
Killdeer	*Charadrius vociferus*
Mourning Dove	*Zenaida macroura*
Red-headed Woodpecker	*Melanerpes erythrocephalus*
Eastern Kingbird	*Tyrannus tyrannus*
Horned Lark	*Eremophila alpestris*
Barn Swallow	*Hirundo rustica*
Blue Jay	*Cyanocitta cristata*
American Crow	*Corvus brachyrhynchos*
American Robin	*Turdus migratorius*
European Starling	*Sturnus vulgaris*
House Sparrow	*Passer domesticus*
Red-winged Blackbird	*Agelaius phoeniceus*
Common Grackle	*Quiscalus quiscala*
Brown-headed Cowbird	*Molothrus ater*
Northern Cardinal	*Cardinalis cardinalis*
Indigo Bunting	*Passerina cyanea*
Dickcissel	*Spiza americana*
Savannah Sparrow	*Passerculus sandwichensis*
Vesper Sparrow	*Pooecetes gramineus*
Chipping Sparrow	*Spizella passerina*

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VARIATIONS IN DIETS OF NESTING COMMON RAVENS

RICHARD B. STIEHL[1] AND STEVEN N. TRAUTWEIN[1]

ABSTRACT.—We investigated variation in the diets of Common Ravens (*Corvus corax*) nesting near Malheur National Wildlife Refuge in southeastern Oregon in the spring and summer of 1976 and 1977. We made microscopic examinations of 1413 regurgitated pellets and other nondigested remains collected near the nests. Mammals, primarily rodents and lagomorphs, made up 39.2% of the sample. Birds (including eggs) comprised 37.8% of the diet. Management of Common Ravens as potential nest plunderers requires a detailed analysis of diets, but the low mean numbers of egg remains (1.33 ± 1.5) found at nests within sagebrush suggests that ravens selecting this type of nesting habitat are probably not nest plunderers. The wide variability in the frequency of eggs in the diets of ravens nesting in wetland habitats suggests that no general assumptions may be made concerning their roles as predators on waterfowl eggs. *Received 7 June 1988, accepted 1 Oct. 1990.*

Studies of the food habits of the Common Raven (*Corvus corax*) have come largely from Europe (Feilden 1909a, b; Lockie 1955; Mylne 1961; Ratcliffe 1962; Holyoak 1968). However, raven diets have been documented in Virginia (Harlow et al. 1975), Wyoming (Dorn 1972), and the Arctic slope of Alaska (Temple 1974). Conner et al. (1975) and Conner and Adkisson (1976) noted that some ravens relied on carrion from road kills and garbage dumps for food. Nelson (1934) investigated the food preferences of ravens in southeastern Oregon, and Maser (1975) noted predation by ravens on Rock Doves (*Columba livia*) in the same general area. These studies indicate that Common Ravens are omnivorous and opportunistic feeders. Ravens also are active predators (Temple 1974), scavengers (Feilden 1909b, Dorn 1972, Conner and Adkisson 1976), and nest plunderers (Nelson 1934). Reports by Dorn (1972), Harlow et al. (1975) and Ratcliffe (1962) suggest that ravens consume at least some vegetable material and Ross (1925) reports the influence of domestic livestock production on the diet of Common Ravens. Predation of ravens on eggs has been classified as a persistent and sometimes serious problem for waterfowl management (Braun et al. 1978). Between 1969–1977, studies at Malheur National Wildlife Refuge indicated that avian predators destroyed approximately 20% (range 8% to 41%) of waterfowl and Sandhill Crane (*Grus canadensis*) nests (Littlefield 1975). Although potential avian predators of eggs in the area include Common Ravens, California and Ring-billed gulls (*Larus californicus* and *L. delawarensis*), Common Crows (*C. brachyrhynchos*), and Black-billed Magpies (*Pica pica*), Braun et al.

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(1978) suggested that Common Ravens were the major avian egg predators, perhaps because ravens are considered more numerous on the refuge than are the other species. Nelson (1934) made a limited study of the stomach contents of ravens collected during June in southeastern Oregon and found a great diversity of food items, but his study was limited to a small portion of the waterfowl nesting season. We report here on food habits of the nesting population of Common Ravens from February through August.

STUDY AREA AND METHODS

The study area included Malheur National Wildlife Refuge located in Harney County, Oregon, U.S.A. This large (73,250 ha) area is about 118 to 119°W longitude and 42 to 43°N latitude at an elevation of 1350 m. The major land forms consist of alkaline lakes and marshlands covering 32,400 ha, river valley uplands supporting *Carex* and other submerged and emergent flora, and extensive rimrock areas of volcanic and fault block origin. On the plateaus of the surrounding area above the rimrocks, typical Great Basin desert vegetation of sagebrush (*Artemisia* sp.) and greasewood (*Sarcobatus* sp.) form the dominant communities. The extensive rimrock formations provide locations for nest sites and suitable habitat for a nesting population of 40 to 50 pairs of Common Ravens (Stiehl 1978, 1985).

Regurgitated pellets comprised the majority of the 1413 food items collected near 32 active raven nests from 1 March to 15 July 1976 and 28 February to 31 July 1977. A nest-centered plot about 20 m in diameter was searched for pellets and other debris (e.g., skeletal remains and egg shells) at least once per week throughout the study periods. Collected materials were sealed in plastic bags, which were dated and identified. Pellets were air-dried, weighed, and dissected with the aid of a 7×–30× stereo microscope. The number of different food items was recorded for each pellet. Hair and bone fragments were identified by comparison with reference material from the mammal collection at Portland State University, or from pellets collected from captive wild ravens fed known diets, or keyed using Hall and Kelson (1959), Ingles (1965) or Verts (1971). Eggshell fragments were identified by comparison to specimens in the collection at Malheur National Wildlife Refuge or keyed to species using Reed (1965). Fish were identified by comparison of scales or skeletal remains to known representatives.

We used the frequency of occurrence data in our analysis, as dissimilarities in compaction and density made it difficult to assign importance to volumetric differences. We identified and separated the items into seven groups: avian eggs; avian feathers and bones; mammal bones, teeth and hair; reptile bones and scales; fish bones and scales; insect body parts; and vegetation. We made the distinction between avian eggs and feathers/bones in order that active nest plunderers could be ascertained. Some obvious potential food sources, such as carrion from large mammals [e.g., domestic cattle (*Bos taurus*) and mule deer (*Odocoileus hemionus*)], are probably not proportionally represented when using only pellets and fragments in an analysis. In pellets, hair would comprise the only remains and is probably only ingested incidentally and in small amounts. Although cattle and deer have a considerable amount of nondigestible material (e.g., bone and hair), the bones are rarely, if ever, transported to the nest site. Our analysis also includes whole eggshells and bones of medium sized mammals (e.g., *Lepus*) collected in the areas near nest sites. Our analysis may be biased in favor of such items because they are large and more obvious in the field. Therefore, they are more likely to be collected. Thus, analysis based on pellets and other nondigestible materials contains inherent biases that will affect conclusions based on the data.

We then assigned each nest site to one of four categories, based on the general habitat surrounding the nest site and on the presence or absence of roads within 0.5 km of the nest site. We formed four unequal nest groupings. We partitioned wetland (WT) habitat nests as either wetland near road (WR) or wetland non-road (WN). Likewise we classified nests in sagebrush (SB) as either sagebrush near road (SR) or sagebrush in a non-road area (SN). The division of habitats into road and non-road areas is important because of the possibility for extensive carrion feeding by pairs nesting near roads. Carrion feeding was also considered important by Feilden (1909a, b), Nelson (1934), Mylne (1961), Ratcliffe (1962), Temple (1974), Harlow et al. (1975), and Conner and Adkisson (1976). Statistical analyses of the data (including ANOVA, Duncan's multiple range test, and *F*-test) were performed with the General Linear Models procedure of the Statistical Analysis Systems (SAS 1982).

RESULTS

Pellet analysis.—Pellets weighed an average of 2.8 g (range 1.6 to 4.7 gm) and contained one to five items. Table 1 summarizes the total occurrence and percent occurrence (number of items divided by total items × 100) for each category of items collected. As a group, mammalian food items had the highest occurrence (898/2202) and comprised 40.8% of the constituents in the sample. This type of food item was found in every nest of the sample population. Smaller mammals, including voles (*Microtus* sp.), mice (*Peromyscus* sp., *Paragnathus* sp., and *Reithrodontomys megalotus*), kangaroo rat (*Dipodomys* sp.), pocket gophers (*Thomomys* sp.), ground squirrels (*Spermophilus* sp. and *Ammospermophilus leucurus*), and shrews (*Sorex* sp.) comprised the largest component (59% or 530/898) of the mammalian constituent. The medium-sized mammals comprised 29.8% (268/898) of the mammalian food collected but contained the highest occurrence for a single species. Black-tailed jackrabbit (*Lepus californicus*) occurred 244 times, which was 11.1% of the mammalian food items. Also included in the medium-sized mammals were muskrat (*Ondatra zibethicus*) and yellow-bellied marmot (*Marmota flaviventris*). Large mammals were represented by hair from domestic cattle (*Bos taurus*) and mule deer (*Odocoileus hemionus*) and comprised only 2% (18/898) of the mammalian component. This may be biased low due to the relatively low proportion of nondigestible material associated with such food which is ingested or transported to the nest. Unidentified mammals had a percent occurrence of 9.1% (82/898) and comprised 3.7% (82/2202) occurrence in the diet of the sample population.

Avian food items identified in the sample consisted of egg shells, bones or other fragments, feathers, and down. The avian-based food items constituted 38.4% (845/2202) of the diet based on percent occurrence. Although avian food items occurred in samples from all nest sites, the distribution did not appear to be even. The occurrence of avian items in the samples collected at nest sites ranged from 1.7% of the sample at one

TABLE 1
ANALYSIS OF PELLETS FOUND NEAR NESTS OF COMMON RAVENS

Species/item	Occurrence	% Occurrence
Avian		
Eggs	535	24.3
Feathers	245	11.1
Avian bones	52	2.4
Avian down	13	0.6
Mammalian		
Lepus californicus	244	11.1
Microtus sp.	208	9.4
Rodentia	115	5.2
Microtinae	90	4.1
Unidentified mammal	82	3.7
Peromyscus sp.	40	1.8
Ondatra zibethicus	22	1.0
Bos taurus	17	0.7
Dipodomys sp.	14	0.6
Lagurus curtatus	13	0.6
Reithrodontomys megalotus	13	0.6
Thomomys sp.	12	0.5
Perognathus sp.	9	0.4
Spermophilus sp.	3	0.1
Marmota flavaventris	2	0.1
Sorex sp.	2	0.1
Mustela sp.	1	Trace
Odocoileus hemionus	1	Trace
Ammospermophilus leucurus	1	Trace
Neotoma sp.	1	Trace
Reptilian		
Reptile parts	25	1.1
Fish		
Cyrpinus carpio	131	5.9
Fish (non *C. carpio*)	42	1.9
Insects		
Insect parts	188	8.5
Vegetation		
Plant material	78	3.5
Unidentified	3	0.1

nest site to 86.7% of the sample at another nest site. Six of the 32 nest sites accounted for 61.5% (520/845) of all the avian items collected. Egg shell remains found near the nest sites accounted for 63.3% (535/845) of the avian food and 24.3% (535/2202) of the diet. Other items collected (feathers and skeletal parts) comprised 36.7% (310/845) of the avian food and 14.1% (310/2202) of the total diet. Of the 2202 food items we analyzed, avian egg shells occurred 535 (24.3%) times. At least some avian egg shell was present in the collected items from 90.6% (29/32) of the pairs studied and ranged from 0% to 84.8% of the collected items at a nest site. Six of the 32 adult pairs studied accounted for 72.5% of the total egg shells collected. The importance of this food source may be overestimated, as nearly intact egg shells are easily located in the field. Whole egg shells collected near the nest sites accounted for 58.3% of the egg shell constituent and 14.2% of the total items collected. Waterfowl eggs comprised 48.8% (261/535) of the eggs collected and were collected at 21 of the 32 nest sites studied. Collections at four nest sites accounted for 72.4% (189/261) of the waterfowl eggs collected. Cinnamon Teal (*Anas cyanoptera*) comprised 39.8% (104/261) of the sample, followed by Gadwall (*A. strepera*) (73 [27.9%]), and Mallard (*A. platyrhynchos*) (46 [17.6%]). Other waterfowl species represented included Canada Goose (*Branta canadensis*), Northern Pintail (*A. acuta*), American Wigeon (*A. americana*), Redhead (*Aythya americana*), Ruddy Duck (*Oxyura jamaicensis*), and Canvasback (*A. valisineria*). The sample also included eggs of Ring-necked Pheasant (*Phasianus colchicus*), Common Raven, Killdeer (*Charadrius vociferus*), American Coot (*Fulica americana*), Wilson's Phalarope (*Phalaropus tricolor*), Long-billed Curlew (*Numenius americanus*), Sandhill Crane (*Grus canadensis*), American Avocet (*Recurvirostra americana*) and American Bittern (*Botaurus lentiginosus*).

Another indication of the use of avian food was the presence of feathers, down, and skeletal remains in the collection. Feathers constituted 29.0% (245/845) of the avian based and 11.1% (245/2202) of the total items collected. Skeletal remains comprised 6.2% (52/845) of the avian and 2.4% (52/2202) of the total. Down had a 1.6% (13/845) avian occurrence and 0.6% (13/2202) total occurrence in the sample. Most of the feathers and down were too decayed to be identified with certainty. Of 310 items, only 74 (23.9%) could be identified to species. Of the material that could be identified, 17.6% (13/74) was waterfowl (Cinnamon Teal, Gadwall, Mallard, and Canada Goose), but also included American Coot, and Sandhill Crane. Some of the feathers and skeletal items may reflect scavenging from carrion or theft from other predators.

The combined remains of insects, fish, vegetation, and reptiles had a 21.1% (464/2202) occurrence in the sample population. Remains occurred

TABLE 2
MEAN FREQUENCY OF GROUPED FOOD ITEMS IN THE DIETS OF COMMON RAVENS IN FOUR HABITATS

Food group	Habitat groupings (N)[a]						
	AN(32)	WT(26)	WN(16)	WR(10)	SB(6)	SN(2)	SR(4)
Eggs	16.1	19.3	18.6	20.4	1.8	0.5	2.5
Birds	9.3	9.9	10.2	9.4	6.9	1.0	9.8
Mammal	26.7	22.8	23.6	21.5	44.1	12.0	60.2
Reptile	0.7	0.6	0.3	0.6	2.2	0.5	3.0
Fish	5.2	6.1	8.1	2.6	1.2	0.0	1.8
Insect	5.6	4.3	4.6	3.8	11.7	6.0	14.5
Vegetation	2.4	2.2	2.2	2.1	3.2	3.5	3.0

[a] AN = All nest sites studied; WT = All wetland nest sites; WN = Wetland nest sites away from roads (non-road); WR = Wetland nest sites near roads; SB = All sagebrush (upland) nest sites; SN = Sagebrush nest sites away from roads (non-road); SR = Sagebrush nest sites near roads.

at 78.1% (25/32) of the nest sites with insects in the diet. We did not attempt to identify the insects, but beetle (Coleoptera) elytra were quite common. Fish remains (scales and bones) were found 173 times (7.9% occurrence) and occurred at 23 (71.9%) of the nest sites. Most (131/173 = 75.7%) of the fish represented were carp (*Cyprinus carpio*). Of those nest sites which had fish in the diet, the occurrence ranged from 0.6% to 30.0%. Vegetation, in the form of partially digested grasses, was found at 18 (56.2%) nest sites and comprised only 3.5% (78/2202) occurrence in the diet of the sample population. Some of the vegetation in the sample may have resulted from the incidental ingestion of nest lining materials during nest building (Stiehl 1985). We suspect that much of the vegetation in pellets was ingested during consumption of stomachs of herbivores

TABLE 3
COMPARISON OF OCCURRENCE OF FOOD TYPES FROM ALL HABITAT TYPES

Food type	Mean number of items	Grouping[a]
Mammal	17.8	A
Eggs	11.2	B
Birds	6.0	C
Insects	3.6	C
Fish	3.0	C
Vegetation	1.6	C
Reptile	0.6	C

[a] Means with the same letter grouping are not significantly different ($P < 0.05$, Duncan's multiple range test).

TABLE 4
COMPARISON OF MEAN NUMBER OF MAMMAL PIECES FOUND IN THE FOUR HABITAT TYPES

Habitat type	Mean number of items	Grouping[a]
SR	42.2	A
WN	14.9	B
WR	14.8	B
SN	7.5	B

[a] Means with the same letter grouping are not significantly different ($P < 0.05$, Duncan's multiple range test).

(e.g., *Lepus californicus* and *Microtus* sp.). Harlow et al. (1975) reported similar suspicions. Reptilian food items occurred at 11 (34.4%) of the nest sites and comprised 1.1% (25/2202) of the occurrence. No attempt was made to classify further this fraction of the diet. Both snakes and lizards were present in our sample.

Diets based on habitat.—Table 2 summarizes frequency of the occurrence of grouped items from the two habitats (WT and SB), the four areas (WN, WR, SN, and SR) and all the nests studied in the population (AN). The results support the contention that Common Ravens feed opportunistically and suggest that birds which nest in different habitats may have different diets. Although non-random sampling procedures may contribute a bias in this statistical analysis, 94% of the refuge population of nesting ravens was sampled. Considering all nest sites, the mean number of mammal pieces/nest site (17.8) is highest, the mean number of egg pieces/nest site (11.2) is second, and all other food types were third with no significant difference among these other food groups (Table 3). ANOVA further indicated that differences in the number of mammal pieces among the nest sites are attributable to differences among the habitat types and that 34% of the variation in the number of mammal pieces is accounted for by the variation in the type of habitat ($P < 0.01$). Habitat we classified

TABLE 5
COMPARISON OF MEAN NUMBER OF REPTILE PIECES FOUND IN THE FOUR HABITAT TYPES

Habitat type	Mean number of items	Grouping[a]
SR	2.2	A
WR	0.5	B
SN	0.5	B
WN	0.2	B

[a] Means with the same letter grouping are not significantly different ($P < 0.05$, Duncan's multiple range test).

TABLE 6

F-TEST FOR VARIABILITY IN THE NUMBER OF FOOD ITEMS FOUND AT WETLAND NEST SITES VERSUS SAGEBRUSH NEST SITES

Food item	Sagebrush nests			Wetland nests			*F* value	*P*
	N	SD	Variance	N	SD	Variance		
Egg	6	1.52	2.27	26	20.89	436.42	192.26	<0.01
Fish	6	0.98	0.97	26	660.00	43.61	44.96	<0.01
Reptile	6	2.97	3.87	26	0.69	0.48	8.06	<0.01
Insect	6	7.84	61.47	26	3.94	15.54	3.96	<0.01
Mammal	6	23.85	568.67	26	13.16	173.10	3.28	<0.05
Vegetation	6	2.40	8.40	26	2.32	5.38	1.25	n.s.
Bird	6	5.57	31.07	26	6.60	43.53	1.40	n.s.

as SR has a significantly higher number of mammal pieces (42.25) than the other three habitat types (Table 4). The differences between road (WR and SR) habitats and non-road (WN and SN) habitats have no effect on the number of mammal pieces found at a nest site, but more mammal pieces were found in sagebrush (SB) habitats than in wetland (WT) habitats. Even though the differences are not significant, ravens which nest in wetland (WT) habitats appear to consume much more birds (including eggs) than ravens which nest in sagebrush (SB) habitats. For all nesting habitats, mammals and birds comprise the majority of the diet and reflect the largely carnivorous diet of the Common Raven. In three of the four habitat types, reptiles comprised the smallest food group. ANOVA showed that the variation in the number of reptile pieces among nest sites is attributable to variations among habitat types. Habitat we classified as SR has a significantly higher number of reptile pieces (2.2) than the other

TABLE 7

F-TEST FOR VARIABILITY IN THE NUMBER OF FOOD ITEMS FOUND AT ROAD NEST SITES VERSUS NONROAD NEST SITES

Food item	Road nest sites			Nonroad nest sites			*F* value	*P*
	N	SD	Variance	N	SD	Variance		
Fish	14	1.73	2.99	18	7.85	61.63	20.61	<0.01
Reptile	14	1.52	2.31	18	0.57	0.33	7.00	<0.01
Mammal	14	21.14	446.86	18	10.85	117.70	3.80	<0.01
Insect	14	6.64	44.11	18	3.50	12.24	3.60	<0.01
Bird	14	7.37	54.34	18	5.73	32.81	1.66	n.s.
Egg	14	20.06	402.59	18	19.42	377.29	1.07	n.s.
Vegetation	14	2.41	5.79	18	2.45	6.02	1.04	n.s.

three habitat types (Table 5). Thirty-three percent of the variation in the number of reptile pieces is accounted for by the variation in the type of habitat ($P < 0.01$). We found no significant difference in the number of vegetation items among the habitat types. It is found infrequently in all habitats except sagebrush (SB). The differences in the diets were analyzed by comparing the variability within the number of food items of each food group found among all habitats. These analyses are summarized in Table 6 and Table 7. Table 6 reveals significant differences in the amount of variation in the number of food items (egg, mammals, reptile, fish, and insects) between wetland habitats (WT) and sagebrush habitats (SB) ($P < 0.01$). Ravens which nest in wetland habitats are apparently more variable in their consumption of eggs and fish. Ravens which nest in sagebrush habitat are apparently more variable in their consumption of mammals, reptiles, and insects. We found no significant differences in the variability in the number of bird and vegetation food items between wetland and sagebrush habitats. When we compared the differences in variability between non-road locations (WN and SN) and road locations (WR and SR), we found significant differences ($P < 0.01$) in the variation in the number of food items of mammal, reptile, fish, and insect origin (Table 7). Regardless of the ecological habitat (wetland or sagebrush), Common Ravens which nest near roads apparently have greater variability in their consumption of mammals, reptiles, and insects. Ravens which use nest sites away from roads apparently have greater variability in their consumption of fish. We found no significant differences in the variability in the number of bird, egg, and vegetation food items between road and nonroad areas.

Our analysis of the data indicates that although there is great variation in the diets of Common Ravens near Malheur National Wildlife Refuge, certain conclusions may be made which may be useful in their management in relation to waterfowl nesting success. The low mean number of eggs (1.33 ± 1.5) in sagebrush areas (SB and SR) suggests that ravens nesting in these habitats have little impact on waterfowl nests through nest plundering. The higher mean (13.5) for nest sites in wetland habitat indicates that nest plundering does occur in these habitats, but the high variability (SD = 20.89, see Table 6 and 7) suggests that only some of the ravens nesting in wetlands are nest plunderers. If reduced waterfowl nest predation is a management objective, then Common Ravens nesting away from wetland areas should receive minimal attention. Further, ravens nesting in wetland areas may or may not be serious threats to waterfowl production. For effective and prudent management of nest plunderers, a more detailed analysis of the diet of the ravens nesting near a waterfowl production area must be completed. Such an analysis of the diets may provide a basis for selective control of predators on National Wildlife Refuges as suggested by Braun et al. (1978).

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SHORT COMMUNICATIONS

Song types of Black-throated Green Warblers on migration.—It is widely known that passerine birds of many species sing while on migration (Armstrong 1973), yet little attention has been paid to the role that their songs might play. In common with some other vocalizations given outside of the breeding season, they might be used as "practice" for the breeding season (e.g., Nottebohm 1975). Alternatively, since some migrating birds hold temporary territories (Rappole and Warner 1976), their songs might serve a defensive function. However, many New World warblers (Parulinae) that remain at migratory stopover sites only briefly, and are therefore unlikely to establish territories (see Rappole and Warner 1976), may sing as well. The role of song in these birds is uncertain. The Black-throated Green Warbler (*Dendroica virens*), a species that sings during migration, has two distinct songs, which are presented in different contexts on the breeding grounds (Morse 1967, 1970, 1989a). There, one has a basically intrasexual role and the other an intersexual role (also see Highsmith 1989, Kroodsma et al. 1989). Thus it is of interest to know which songs they give on migration, since this information might provide insight into the role that song plays at this time. I report here on the song types given by Black-throated Green Warblers on spring migration in Maryland and Rhode Island. The Rhode Island site lies about 500 km northeast of the Maryland site and is closer to the breeding grounds than the latter.

Methods.—I counted song types in Prince George's Co., Maryland, during the spring migrations of 1976–1978, and E. S. Morton and R. Greenberg did so for me in neighboring Washington, D.C. (8 km southwest), in 1986–1987. I subsequently refer to these two locations as the Maryland sites. I also tabulated song types in Providence, Providence Co., Rhode Isand during the 1983–1988 spring migrations. Since Black-throated Green Warblers do not nest in the immediate vicinity of either study area, all of the birds can be classified as migrants. Song types were counted on the breeding grounds (Bremen, Lincoln Co., Maine) during late May of 1966 and late June–early July of 1971.

All observations were made in the morning, from 0700 to 0900 in clear or partly cloudy weather. Songs were identified as to type, and for most birds the number of songs given over two minutes was recorded. Sound spectragrams of the Black-throated Green Warblers' two song types, here called Accented Ending and Unaccented Ending songs, appear elsewhere (Morse 1967, 1970, 1989a). The former plays an important intersexual role on the breeding grounds, and the latter a basically intrasexual role (see Kroodsma et al. 1989). Individuals were counted only once at a site during a morning, and since conspecifics were seldom present at a site on successive days, the number of individuals listed is unlikely to differ appreciably from the actual number of individuals. The birds were not marked, however.

Results.—Unaccented Ending Songs dominated in Maryland, both in numbers of birds singing and in total songs (Table 1). In contrast, Accented Ending Songs were most frequent in Rhode Island, although their relative dominance did not match that of Unaccented Ending Songs in Maryland. The difference between the two sites was significant, both for the number of birds singing the two songs ($G = 8.45$, df = 1, $P < 0.01$) and for the total number of songs of the two types given in the sample available ($G = 34.45$, df = 1, $P < 0.001$). The singing Black-throated Green Warblers that I observed occurred at low densities, with only a single individual noted on most days (Table 1) and more than one singing bird in the same area noted only twice.

This difference in song types could have resulted either from the later dates of observation in Rhode Island, or in the time remaining to reach the breeding grounds. Observation dates for Rhode Island birds (May 13.5 ± 4.7 days) ($\bar{x}$ ± SD) averaged 6.2 days later than those in Maryland (May 7.3 ± 7.7 days), presumably reflecting differences in migration times.

TABLE 1

ACCENTED ENDING SONGS (AES) AND UNACCENTED ENDING SONGS (UES) GIVEN IN MIGRATION BY BLACK-THROATED GREEN WARBLERS

Site and year	Number of birds[a]			Number of songs		AES/ UES	Songs/ min
	AES	UES	Both	AES	UES		
MD, 1976–1978	1	7	1	2	29	0.1	1.7
MD, 1986–1987	3	10	0	—	—	—	—
RI, 1983–1988	11	6	0	64	37	1.7	3.0

[a] The birds were observed on seven different mornings in Maryland (MD) (1976–1978) and 11 different mornings in Rhode Island (RI). The data are not available for Maryland (1986–1987).

Overlap of times was inadequate to compare song types in the two areas on given days, but Rhode Island birds did not differ in the dates on which they sang the two song types (Accented Ending = May 13.4 ± 5.5 days ($\bar{x}$ ± SD), Unaccented Ending = May 13.8 ± 3.2 days; $P > 0.8$ in a two-tailed Mann Whitney *U*-Test). Too few birds sang Accented Ending Songs in Maryland to make this comparison; unfortunately, singing dates were not recorded in 1986–1987. The ratio of Accented to Unaccented Ending Songs is even higher on the breeding grounds in late May, however. In 1966, the ratio of Accented to Unaccented songs was 4.2 to one between 18 and 27 May, at which point Unaccented songs became dominant.

The migrants repeated songs more slowly (Table 1) than birds on the breeding ground during the middle of nesting, which averaged 4.3 ± 1.1 songs/min, N = 25, for Accented Ending Songs, and 5.6 ± 1.1 songs/min, N = 20, for Unaccented Ending Songs. However, the rates of Accented Ending Songs in Rhode Island more closely approximated birds on the breeding grounds than did those singing Unaccented Ending Songs in Maryland.

Although observations on quality of notes or volume are difficult to quantify under field conditions, in several instances songs varied grossly from those typical of the breeding grounds. Specifically, of the 26 birds on which I made such observations, four gave songs missing one or more ending notes. Additionally, four birds gave only songs commonly characterized as "reedy" (2) or "buzzy" (2), highly atypical of songs given during the middle of the breeding season. None of the 40 birds that I timed during the breeding season (five sang both types of songs) gave atypical songs during the periods of measurement. Admitting the possible subjectivity of this sample the difference in frequency of atypical songs between the migrating and breeding-ground song samples is highly significant ($G = 16.66$, df = 1, $P < 0.001$).

Discussion.—The difference of song types in the two study areas is of interest, because as the birds move closer to their breeding grounds they increase the frequency and proportion of Accented Ending Songs. On the breeding grounds the Accented Ending Song is the song given when males are with females (Morse 1967), and it also prevails during the early part of the season, apparently before pair formation (Morse 1967, 1970). The data do not address whether time to the breeding ground or time of the year is associated primarily with this shift, but the similarity of singing dates for the two songs in Rhode Island is consistent with impending arrival on the breeding ground assuming primary importance.

Songs on migration were infrequent and intermittent in comparison to those on the breeding grounds, but the frequency of Accented Ending Songs in Rhode Island more closely resembled that of the breeding grounds than did Unaccented Ending Songs in either location. This is consistent with the birds' approaching the condition attained on the breeding grounds at the beginning of the year.

The increase in frequency of vocalizations between Maryland and Rhode Island suggests that the birds are bringing their singing patterns to a frequency resembling that of the breeding season. I do not have comparable singing rates of individuals when they first reach their breeding grounds; however, high rates may not always characterize their arrival. In the congeneric Prairie Warbler (*D. discolor*), Nolan (1978) noted that some recent arrivals showed little tendency to sing or exhibit other signs of territorial proclamation, which he attributed to inadequate physical condition resulting from migration.

Taken together, these results suggest that over the migration period, song is changing in a way that comes to resemble the patterns predominant at the beginning of the breeding season. In the absence of any observations of close contact between singing males and females on migration during this study, it does not seem appropriate to attribute the vocalizations at this time directly to courtship activities. Although the migratory periods of male and female Black-throated Green Warblers do overlap, substantial numbers of males may precede most females (see Morse 1989b). The absence of females resembles the males' arrival on their breeding grounds, since they generally precede females (Morse 1989b). Thus, although considerable information suggests that Accented Ending Songs play an important intersexual role, it is likely that they assume predominance in the immediate absence of the females. Their use, both in the absence of females and other males, is consistent with Kroodsma et al.'s (1989) hypothesis that Accented Ending Songs can act as "default" songs as well as ones with a direct intersexual message. It is more difficult to fit the contexts of Unaccented Ending Songs, as well as the differences in proportions of the two song types, into this argument, especially the predominance of Unaccented Ending Songs in Maryland in the absence of other males.

These observations were notable for the number of abnormal songs in comparison to the middle of the breeding season, both in the number of incomplete songs, an easily quantifiable character, and in "qualitative" differences that could not be quantified without acoustical analysis. These variations also increase in relative frequency at the end of the nesting season on the breeding grounds (Morse 1967). The relatively high frequency of imperfect and incomplete songs during migration resembles that reported for a wide variety of both Nearctic and Palearcitc species (see Armstrong 1973).

Several species of paruline warblers give two or more songs that differ in context in a way that appears similar to the Black-throated Green Warbler (e.g., Ficken and Ficken 1969, Lein 1978, Nolan 1978, Morse 1989a). Therefore, it is possible to expand this approach and perhaps cast additional light on the role of song in migration. Such investigations should ideally also include songs given on the wintering grounds, since a number of species sing prior to leaving (Armstrong 1973, Morse 1980).

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Avoidance of song matching in the Wood Thrush: a field experiment.—Song matching is a common form of vocal interaction in oscine species. It occurs when one bird, typically a territorial male, answers the song of another bird with a similar song. Matching has been reported for many species in which males sing with "eventual variety," uttering one version of the territorial song a number of times before switching to another version: AAAA . . . BBBB . . . (e.g., Hinde 1958; Gompertz 1961; Lemon 1968a, b; Kroodsma 1971; Krebs et al. 1978). In contrast, matching has been reported for only a few species that sing with "immediate variety:" ABCDE . . . (e.g., Todt 1970, Verner 1975, Kroodsma 1979). It is not possible to say from present evidence whether matching is truly less common in birds that sing with immediate variety, but there is a clear need for studies of these species.

Wood Thrushes (*Hylocichla mustelina*) sing with immediate variety. My objective in the study reported here was to determine whether the results of an earlier study (Whitney and Miller 1983, see also Whitney 1985) of song matching in captive Wood Thrushes could be generalized to free-ranging birds. In the earlier work I presented each male with recordings of songs that were structurally similar to one of his own songs but that varied systematically from it in frequency (Hz). The results indicated that matching is related inversely to song similarity: the more similar the stimulus song was to the bird's own song, the less it was matched, to the extent that subjects avoided matching their own songs and songs very similar to them.

Materials and methods.—A typical Wood Thrush song has three phrases, referred to as the A, B, and C phrases. The introductory A phrase consists of one or more low-pitched sounds, the middle B phrase is of loud flute-like notes, and the ending C phrase is usually a trill. B phrases are learned from conspecifics (Whitney and Miller 1987b) and can be classified into discrete types (Whitney and Miller 1987a, Whitney 1989). Use of the term "song type" in this paper refers to these B phrases. Each male has a repertoire of 2–8 B phrases, several of which may be different versions of the same type.

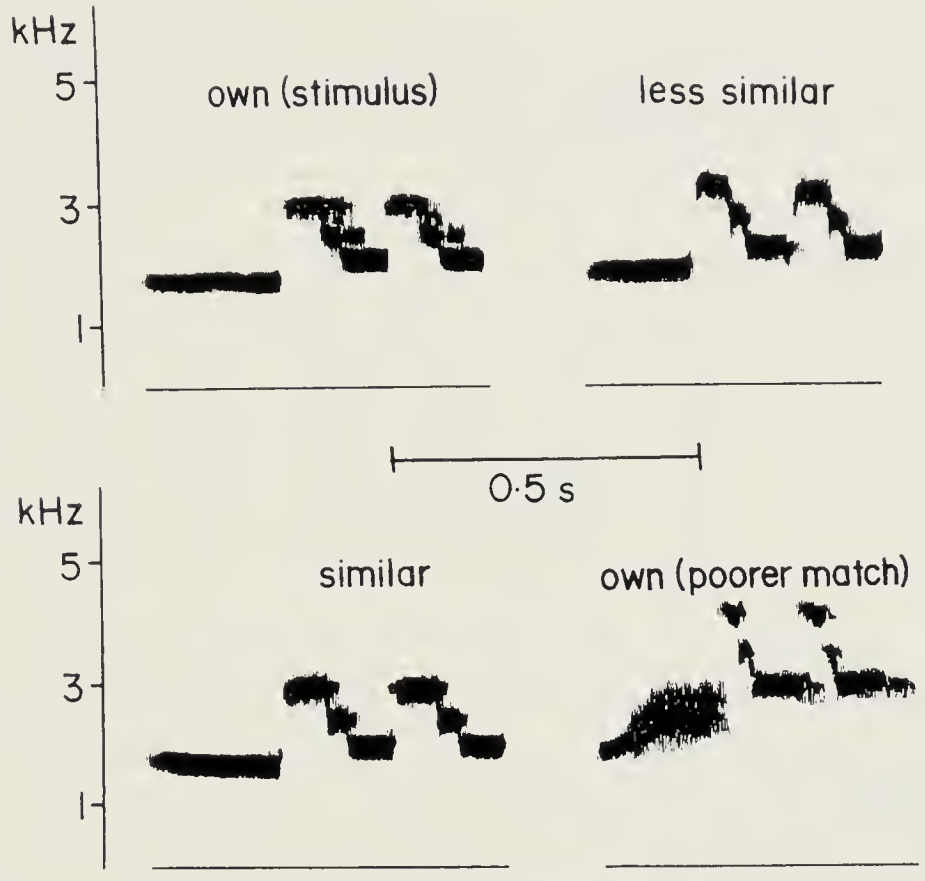

FIG. 1. Songs (each consisting only of a B phrase) presented to subject E, and a second song ("poorer match") of the same type in the subject's repertoire.

The experiment, done from 27 May to 21 June 1982 at 0530 to 0800 EDT, tested the response of territorial males to three songs: (1) a song from the subject's own repertoire, (2) a song of the same type as the subject's own song and very similar to it, and (3) another song of the same type but less similar to the subject's own song. Each stimulus song consisted only of a B phrase. I judged similarity of songs on the basis of frequency (Hz), requiring that each note of the "similar" song (category 2) be at least 200 Hz more similar in frequency than that of the "less similar" song to the corresponding note of the subject's own song. Fig. 1 shows the songs played to one subject.

The stimulus presented to each subject in the "own" song treatment was, of course, unique. For the "similar" and "less similar" treatments, however, subjects C and E (see Table 1) were presented with the same pair of songs, as were subjects D and F. Thus, the experimental design fell slightly short of Kroodsma's (1989) recommendations.

The general procedure was to broadcast a stimulus song from a loudspeaker in a subject's territory. Specific procedures were very similar to those used by Whitney and Miller (1983) in the earlier experiments with captive Wood Thrushes. On a given day the subject would hear 75 playbacks of one of the three stimulus songs. Each playback was of a single rendition of the song and occurred with a latency of 0.5–2.0 sec after the subject had completed one of his own songs. The subject was allowed to sing a randomly determined number (3, 4, 5, or 6) of songs between successive playbacks. For each subject the order of the experimental treatments was randomized, and the playbacks were done, one treatment per day, over a three to five day period. Thus, individual subjects were "blocks" in a randomized block

TABLE 1

RESULTS OF PLAYBACK EXPERIMENT (O/E = OBSERVED/EXPECTED NUMBER OF MATCHES; N = 75 PLAYBACKS FOR EACH TRIAL; CHI-SQUARE VALUES ARE FOR ONE DEGREE OF FREEDOM)

	Own song			Similar song			Less similar song		
Subject	O/E	χ^2	*P*	O/E	χ^2	*P*	O/E	χ^2	*P*
A	0.28	15.74	<0.001	0.20	23.73	<0.001	0.32	11.80	<0.001
B	0.77	1.40	N.S.	1.08	0.16	N.S.	1.33	2.63	N.S.
C	1.04	0.05	N.S.	0.97	0.03	N.S.	0.67	3.86	<0.05
D	0.65	2.42	N.S.	0.89	0.24	N.S.	0.91	0.16	N.S.
E	0.24	8.66	<0.005	0.86	0.36	N.S.	0.62	2.18	N.S.
F	0.16	10.12	<0.005	0.97	0.01	N.S.	0.38	6.30	<0.025
G	0.64	1.91	N.S.	0.85	0.33	N.S.	0.62	2.22	N.S.

design (e.g., Zar 1984). Anticipating a great deal of variability among subjects in their matching response (variability due perhaps in part to differences in breeding status, a variable that I did not measure), I chose this experimental design in order to increase statistical power in testing for a difference among song treatments.

I recorded the following data during each experimental trial: (1) the total number of songs sung by the subject, (2) the total number of renditions of the song of the same type as the stimulus song, and (3) the number of times the stimulus song was matched.

The subjects were seven males holding territories on or near the grounds of the Rockefeller University Field Research Center, Millbrook, New York. Immediately before doing the first playback to each male, I observed his behavior for at least 30 minutes and noted the locations of all song posts. I placed the loudspeaker on or near the ground within the area defended by song, using the same location for all trials. I controlled the loudspeaker from a distance of 15–20 m.

Throughout each experimental trial, I recorded the distance of the subject from the loudspeaker. To aid in estimation of distance I placed a pole 5 m from the loudspeaker.

The songs used for playback had been recorded with either a Uher Report IC tape recorder or a Sony TC-D5M cassette recorder, each equipped with a Dan Gibson P650 parabolic reflector and microphone. The playback system included a Sony Walkman Professional tape recorder, a Realistic 40W amplifier, and a Realistic 12-1853 loudspeaker.

The sonagrams (Fig. 1) were prepared with a Macintosh Plus computer, a MacADIOS 411 hardware unit, a TTE 411AFS amplifier and anti-aliasing system, and MacSpeech Lab software (GW Instruments). The recording sample rate of the system was set at 10.416 kHz (according to which rate the maximum frequency displayed on a sonagram is 5 kHz), and the wide band filter (300 Hz) was used.

Results.—In most trials the subjects sang continually, except during flights. By allowing the subjects to sing a randomly determined number of songs before each playback, I established the expectation that by chance alone the number of playbacks answered with a given song type should be proportional to the overall frequency of occurrence of that song type.

In 18 of 21 trials the observed number of matches to the stimulus song was less than the expected number ($P < 0.002$, two-tailed binomial test). Several subjects were presented with the same songs in the "similar" and "less similar" treatments. The results were combined appropriately, resulting in 17 independent trials; the observed number of matches was less

than expected in 14 of these ($P < 0.02$, two-tailed binomial test). None of the stimulus songs was matched significantly more often than expected by chance, but seven were matched significantly less often (Table 1). Three of these seven songs were the subjects' own songs, one was a "similar" song, and three were "less similar" songs.

A Friedman's nonparametric analysis of variance for the randomized block design (Zar 1984) revealed no difference in the response to the three classes of songs ($\chi^2 = 2$, df = 2, $0.50 > P > 0.25$).

Having memorized the song repertoires of subjects D and F before starting the experiment, I was able to keep complete records of the songs they sang during each trial. As shown in Table 1, subject D did not match his own song significantly less than expected. Overall, however, his use of the four songs in his repertoire to answer his own song did deviate significantly from the expected ($\chi^2 = 12.48$, df = 3, $P < 0.01$). Similar analysis of the remaining three trials in which these two birds matched neither more nor less often than expected by chance revealed no further significant results.

According to the system used in classifying song types (Whitney and Miller 1987a), subject E had two songs in his repertoire of the same type as the stimulus songs. One of these songs was clearly a poorer match to the stimulus songs (Fig. 1). In all three trials the subject favored answering the stimulus with this song (Observed/expected number of matches = 1.66, 1.56, 1.49, respectively); with data combined for all trials, the result was significant ($\chi^2 = 12.52$, df = 1, $P < 0.001$).

Because each trial of the experiment involved 75 playbacks and lasted for 20 minutes or more, one can wonder whether the matching response of the subjects was consistent throughout this lengthy period. In an attempt to answer this question, I did two analyses. First, I calculated the ratio of the observed to expected number of matches for the first 20 playbacks and last 20 playbacks of each trial. If birds habituated during each trial by showing a decreasing tendency to match or avoid matching the stimulus song, this ratio should be closer to unity for the last 20 playbacks than for the first 20. In only 10 of the 21 trials, however, was the ratio closer to unity for the last 20 playbacks.

Second, I applied a runs test (Siegel 1956) to the series of matches and non-matches in each trial. In only three of 21 trials did the results deviate significantly from random: twice matches were clumped (similar and less similar songs for subject A; $P < 0.01$ and $P < 0.05$, respectively), and once they were spaced (similar song for subject B; $P < 0.001$).

Subjects were often out of my view during trials, but I was able to judge their closest approach to the loudspeaker as being in one of the following four categories: 0–5 m, 5–10 m, 10–20 m, and >20 m. In 14 of the 21 trials the subject approached to within 5 m of the loudspeaker. This response occurred in five of the seven trials in which the subject significantly avoided matching the stimulus song and in nine of the 14 remaining trials. Thus, subjects that avoided matching were no more likely than other birds to approach the loudspeaker closely.

Discussion.—The predominant vocal response to playback of recorded songs was avoidance of matching. In earlier research with captive Wood Thrushes, avoidance of matching occurred only when the stimulus song was identical or very similar to one of the subject's own songs (Whitney and Miller 1983). Using a computer to manipulate the frequency (Hz) of songs, I found that a shift of only 156 Hz eliminated the avoidance response of a subject to his own song. A shift of 468 Hz resulted in significant matching. From these results I proposed an inverse relationship between matching and song similarity.

This inverse relationship did not occur in the present research. The subjects were not consistent even in response to their own songs, only three of seven showing significant avoidance of matching (Table 1). Even more surprising was their response to "less similar" songs. Note for note, these songs differed from the birds' own songs by 200–600 Hz, yet

not a single subject matched significantly, and three avoided matching. I found only a single piece of evidence that free-ranging Wood Thrushes might sometimes match less similar songs of the same type: subject E had two songs in his repertoire of the same type as the stimulus songs and favored answering with the one that was a poorer match.

These experimental results, taken together with field recordings I have made of natural vocal interactions (Whitney, unpubl. data), indicate that avoidance of matching is common in free-ranging Wood Thrushes. Does avoidance of matching by territorial Wood Thrushes have functional significance? Could avoidance of matching in this species be functionally equivalent to the matching that occurs in many other species?

According to one hypothesis, matching allows a male to gain the attention of a specific rival (J.-C. Bremond, cited in Armstrong 1973). It seems unlikely that avoidance of matching functions in this way, since avoidance can only be detected over an extended period of time. Imagine two males, one with song A and the other with a similar song A′. If 40% of the songs delivered by the second male during a bout of singing are A′, then it is expected that 60% of the first bird's renditions of A will not be matched when the two birds are singing independently. The first bird would require a large sample of answers to A in order to distinguish between this chance expectation and active avoidance.

Avoidance of matching is rarely so extreme in Wood Thrushes that no matching whatsoever occurs (Table 1 and unpubl. data). Perhaps, one might suggest, avoidance is a background against which a male suddenly matches several times in succession to gain the attention of a rival. Contrary to this idea, however, the temporal order of matches and nonmatches to stimulus songs in the experiment was indistinguishable from the random expectation in 18 of 21 trials.

According to a recent hypothesis, matching functions not just to address a specific rival but to convey information about distance. Upon being matched, a bird would use its own song as a standard for estimating the extent of acoustic degradation—hence distance—of the other bird's song (Richards 1981, Falls et al. 1982, Morton 1982, McGregor and Krebs 1984). This hypothesis obviously cannot account for avoidance of matching, but the possibility remains that Wood Thrushes use a similar method of estimating distance. At present I have no evidence that avoidance of matching in Wood Thrushes represents anything more than a shortcircuiting of the neural mechanism that causes Wood Thrushes to sing with immediate variety. Presented with a stimulus song that is identical or very similar to one of his own, a male often behaves as if he has sung the song himself: he advances to the song that follows it in normal sequences (Whitney 1985).

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Diurnal resting metabolic rates of accipiters.—One of the major sources of error in estimating avian daily energy expenditure with time budgets is the estimate of maintenance metabolism (Weathers et al. 1984, Goldstein 1988, Nagy 1989). Resting metabolic rate (RMR) of a species of interest is often calculated from an allometric equation derived from measurements on other species. For example, Aschoff and Pohl's (1970) allometric equations for non-passerine birds are typically used to estimate active phase and resting phase RMR's of falconiforms (Tarboton 1978, Wakeley 1978, Koplin et al. 1980), but they do not include data from falconiforms. Wasser (1986) demonstrated that the relationship of RMR to body mass during the resting phase of falconiforms does not conform well to the predictions of Aschoff and Pohl (1970).

The RMR during the active phase of the daily cycle is approximately 24% higher than during the resting phase in some non-passerine species (Aschoff and Pohl 1970). Our ob-

jectives were to: (1) measure active phase RMR in accipiters, a group of falconiforms for which few metabolism measurements are available; and (2) compare our empirical results with the predictions from allometric equations in the literature.

Methods.—Metabolism was measured using Sharp-shinned Hawks (*Accipiter striatus*), two females and one male; Cooper's Hawks (*A. cooperii*), three females and two males; Northern Goshawks (*A. gentilis*), one female and one male; and a Black-and-White Goshawk (*A. melanoleucus*), one female. All birds were adults, thus minimizing potential variation in metabolic rates resulting from age class differences.

Five of the accipiters (the Black-and White Goshawk, the two Northern Goshawks, and two of the Cooper's Hawks) were long-term captives from a private breeding and falconry facility in San Diego, California. These birds were maintained in outdoor aviaries under natural conditions of temperature and photoperiod. The metabolism measurements of these birds were taken at the San Diego facility during September 1988.

The six additional birds (the three Sharp-shinned Hawks, and three of the Cooper's Hawks) were migrants that were trapped in bow nets or mist nets at the southern end of the Goshute Mountains in Elko County, Nevada, during September 1985. The measurements were taken near the trapping site soon after capture and the birds were released after the measurements were completed.

To collect the metabolism measurements, we confined each bird in a metabolism chamber of 4–30 L depending upon the size of the bird. We measured the temperature within the chambers with a copper-constantan thermocouple. The chamber temperatures ranged from 19°C–31°C, within the thermoneutral zone of most raptors (Wasser 1986).

We measured the rate of oxygen consumption ($\dot{V}O_2$ in L O_2 min^{-1}) of each bird in an open-flow system using a portable Ametek S-3A oxygen analyzer that had been calibrated with atmospheric air. We removed carbon dioxide and water from the air stream by circulating the air through Ascarite and Drierite after it exited the metabolism chamber. Air then passed through a rotameter that was calibrated with a Vol-u-meter (Brooks Instrument Division, Emerson Electric Co.) before and after $\dot{V}O_2$ was measured. For each experiment we selected a flow rate between 1.5 and 1.8 L min^{-1} (STPD) depending on the bird's size and the size of the metabolism chamber.

The $\dot{V}O_2$ of a bird was measured for 60–90 min. At the end of a measurement the bird was calm, and its $\dot{V}O_2$ was judged to be in a steady-state. We calculated the rate of oxygen consumption with Equation 4b of Withers (1977) and calculated the rate of metabolic heat production ($\dot{H}_{ma}$ in mW) from $\dot{V}O_2$ by assuming 19.6 kJ of heat is produced per liter of O_2 consumed. This was based on an assumed respiratory quotient (RQ) of 0.7. Gessaman and Nagy (1988) found that errors in converting gas exchange measurements to energy metabolism for uricotelic carnivores were minimized when an RQ of 0.72 was used as compared with higher RQ values.

The San Diego birds were not fed 12–24 hours before the experiment and consequently were in a post-absorptive condition. The absorptive status of the Nevada birds could not be determined with certainty. We assumed these birds were post-absorptive because their crops were empty (determined by palpation). If the migrants were actively digesting and assimilating prey their metabolic rates should have been significantly higher than the captive birds' metabolic rates because of the produced heat increment of feeding.

To test this prediction, we used an analysis of covariance to examine whether or not the migrant metabolic rates were significantly different from the captive birds. Biomass was treated as a covariate in this analysis. The metabolic rates of the wild birds were not significantly different from the captive birds ($F = 1.59$, $P = 0.24$) which supports our assumption that the migrants were fasting when measured.

All experimental measurements were made between dawn and dusk, the active phase of

TABLE 1

METABOLIC HEAT PRODUCTION OF ACCIPITERS DURING THE ACTIVE PHASE OF THE DAILY CYCLE

Species	Sex	Mass (g)	$\dot{H}_{ma}$ (mW)	Aschoff and Pohl (1970)[a]	Wasser (1986)[b]
Accipiter striatus	M	101.0	850.60	827.02	663.88
	F	170.0	1178.63	1208.82	926.43
	F	172.7	1097.47	1222.79	935.82
Avg. females		171.4	1138.05		
A. cooperii	M	286.9	2598.17	1770.32	1295.01
	M	384.0	2434.33	2189.49	1560.63
Avg. males		335.5	2516.25		
	F	436.2	2556.13	2402.69	1693.27
	F	427.8	3079.86	2368.87	1672.33
	F	536.5	2330.50	2793.97	1933.09
Avg. females		466.8	2655.50		
A. gentilis	M	751.0	4281.60	3570.32	2397.38
	F	958.2	3620.94	4264.30	2801.94
A. melanoleucus	F	919.0	3023.14	4136.40	2728.03
Mean deviation from measurements (%)				−0.17	−28.82

[a] Active phase RMR for non-passerine birds calculated from the relation $mW = 28.6M^{0.729}$.
[b] Resting phase RMR for falconiforms calculated from the relation $mW = 34.62M^{0.64}$.

these diurnal raptors. Each bird was weighed to the nearest 0.1 g immediately after each experiment.

Metabolism-body weight relationships are generally presented as allometric equations generated by standard regression techniques (Lasiewski and Dawson 1967, Zar 1969, Aschoff and Pohl 1970). We did not generate an allometric equation because our data were from a small number of species (4) and a narrow range of body sizes (100–958 g). The validity of the relationship of such a narrowly defined allometric equation is questionable (Zar 1969). Differences in metabolic rates between species were evaluated using the analysis of variance. Paired *t*-tests were used to compare the measurements with the predictions of Aschoff and Pohl (1970) and Wasser (1986) for non-passerines and falconiforms, respectively, of equivalent body size.

Results and discussion.—Larger accipiter species had significantly higher rates of metabolic heat production than smaller species (Table 1, $F = 30.26$, $P < 0.01$). Sample sizes were too small for all species to test for significant differences between sexes but mean values for male Sharp-shinned Hawks and Cooper's Hawks were smaller than the mean values for the larger-bodied females.

From regression analysis, Aschoff and Pohl's (1970) relationship between the body mass (M in g) of non-passerine birds and (1) their active phase RMR ($\dot{H}_{ma}$ in mW) can be expressed as:

$$\dot{H}_{ma} = 28.6\ M^{0.729} \qquad (1)$$

and (2) their resting phase RMR can be expressed as

$$\dot{H}_{mr} = 22.4\ M^{0.734}. \quad (2)$$

The mean active phase RMR of accipiters in our study was not significantly different than Aschoff and Pohl's (1970) predictions (Eq. 1) for non-passerine birds of similar mass (Table 1; $t = 1.41$, $P = 0.19$).

Wasser (1986) derived an allometric equation for predicting falconiform RMR during the resting phase of the daily cycle. This relationship expressed in the units of Equation 1 is

$$\dot{H}_{mr} = 34.62\ M^{0.64}. \quad (3)$$

In general, Aschoff and Pohl's equation for non-passerines of similar mass (100–1000 g) predicts a resting phase RMR that is higher than the RMR predicted by Wasser suggesting that most falconiforms, but not accipiters, have a lower resting phase RMR than other non-passerines.

The mean active phase RMR of accipiters was significantly higher (28.8%) than Wasser's (1986) predictions for falconiforms during the resting phase of their diurnal cycle (Table 1; $t = 76.9$, $P < 0.01$). Wasser measured only two accipiters in his study of 22 species of falconiforms; consistent with our results, both of Wasser's measurements were approximately 20% higher than what was predicted by his regression equation.

Although commonly cited as examples of "sit-and-wait" predators (Pianka 1974), recent telemetry studies (Widén 1984, Fischer 1986, Kennedy, 1991 indicate accipiters are very active and do not perch for long periods of time. As a result of these high activity levels, the metabolic rates of accipiters appear to be higher than other falconiforms of similar size throughout the daily cycle.

Since the values of active phase RMR computed from Aschoff and Pohl's equation (Eq. 1) for non-passerines were similar to the RMRs that we measured, it is reasonable to use their equation to predict the RMR of accipiters during the active phase of the daily cycle. Furthermore, Aschoff and Pohl's equation for non-passerines during the resting phase (Eq. 2) may be more appropriate for estimating accipiter resting phase RMR than Wasser's equation for falconiforms (Eq. 3).

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Feeding ecology of Chesapeake Bay Ospreys and growth and behavior of their young.—As the Chesapeake Bay's fish population has declined, food may have become more limiting to the bay's Ospreys (*Pandion haliaetus*) (Rothschild et al. 1981, Thompson 1984, Bird 1985). In 1985, we studied Ospreys in southwestern Chesapeake Bay. During this study, it appeared that there was increased sibling aggression, brood reduction, and decreased growth of the young compared with 1975 (Stinson 1976, 1977). This paper examines those differences and their apparent cause.

Methods.—Seven Osprey nests in Mathews and Lancaster counties, Virginia, were studied 21 May–25 July 1985. All nests were approximately 25–125 m from shore and accessible by boat. At most study locations, the Ospreys experienced various amounts of human activity (including our own), but they appeared to habituate to disturbance. Ospreys were observed four days per week. Each day included two, 7.5 h observation periods (0530–1300; 1300–2030 h DST) which were arranged systematically such that we spent 15 h/wk at each nest. We used 20 × 60, 40 × 60 and 40 × 80 scopes for observation. We estimated the size of the fish brought to each nest by comparing them with 48-cm wooden rods graduated at 12-cm intervals affixed to each nest; we used the adult Osprey's tarsus for reference as well.

Fish lengths were converted to grams using length-weight relationships specific for each fish species (McLean 1986). We recorded the number of bites of fish eaten by the nest occupants during three, randomly selected, one-minute periods. We also noted the amount of time each male spent perched near the nest.

We visited the nests twice a week for approximately 10 min per visit to weigh and mark young and to measure lengths of their longitudinal body axis, tail, culmen, and tarsus. Masses were measured with 1000- and 2000-g Pesola spring scales. Crop fullness was estimated by palpation. The ages of the young were known within one day, and, in some cases, the exact date of hatching was noted. In nearly all cases, sex was determined by tail length (MacNamara 1977), behavior (MacNamara 1977), and feather color (Jamieson 1979, Jamieson et al. 1982). Red nail polish was applied to the middle toe of the largest sibling of the brood, and later, picric acid (a harmless dye) was applied to the neck and upper breast feathers to help identify individual young. Once the chicks were several weeks old, they were banded with U.S. Fish and Wildlife Service aluminum leg bands and with unique combinations of colored leg bands for positive identification; band masses were subtracted from all subsequent body mass measurements.

In July 1985, we visited local fish markets to collect samples of the bay's fish included in the Ospreys' diets. Samples were dried for 10 days at temperatures of 55–60°C, ground in a Wiley mill, and pelletized. We used a Phillipson oxygen microbomb calorimeter to determine cal/mg dry weight per sample.

Growth rates of the young were calculated based on logistic models (Ricklefs 1967). We also calculated the inverse of growth, t_{10-90} (days) = 1.098/(dw/dt), which represents the time required to grow from 10 to 90% of its asymptotic weight (Ricklefs 1976). We used one-way ANOVA to test for significant differences among means. Student-Newman-Keuls multiple range tests were used to compare fledging times between broods. All statistical analysis used the SPSSX (SPSSX 1983) and Minitab (Ryan et al. 1985) software packages.

Results.—The male Osprey did virtually all of the hunting and delivered 0.35 ± 0.14 fish/hour (mean ± SD, N = 52). Adult males spent an average of 29.9% ± 15.0 of daylight hours perched near the nest (inactive time).

We observed 32 incidents of sibling aggression in over 640 h of observation. All but one of the multi-young broods had at least one such incident, and eight and 18 aggressive actions occurred in Nests 5 and 7, respectively. Aggression commonly was a peck or a blow delivered to the back of the neck, head, or tail. Such behavior was noted throughout the nestling and fledgling periods. Thirty of the 32 attacks occurred during feeding. Once the aggressive chick appeared to have a full crop, the aggression would usually cease. The aggressor was nearly always the heaviest young, with the exception of the male of Nest 7. Victims of the aggression incurred substantial feather and epidermis injury, loss of access to food, and retardation of growth. In 35 of 48 feedings, the subordinate young in Nests 5 and 7 received no food at all. Such food deprivation likely was responsible for the early death of the smaller young of Nests 5 and 6. In general, a marked disparity was evident between the dominant and subordinate young in terms of size, mass and overall appearance of health (see below).

Sibling aggression (the number of blows) was not correlated significantly with the wet mass (g) of prey delivered to the nest ($r = 0.665$, df = 5, $P > 0.05$). However, sibling aggression and the caloric value of delivered prey were significantly correlated ($r = 0.754$, df = 5, $P = 0.05$).

To compare growth rates of Ospreys with those calculated by Stinson (1977), asymptotic values were calculated. Because asymptotic mass near fledging time is inversely proportional to brood size (Stinson 1977), the mean mass of the largest nestling of each brood size was used to represent the asymptote (Stinson 1977). Using 1700, 1605, and 1717 g as the asymptotic weights of one-, two-, and three-young broods, respectively, the growth rate (K) of the 14 young was 0.13 ± 0.04 (N = 14). The time required for the young to grow from

TABLE 1
COMPARISON OF OSPREY NESTS AND YOUNG STUDIED IN 1975[a] AND 1985[b]

Variable	1975	1985
Total number of young	22	16
Total number of nests	10	7
Acts of sibling aggression	0	32
Cases of brood reduction	0	2
Percentage of empty crops	0	55
Sequential feeding of young	yes	no
Rank of young changes	yes	no
Adult males feed young	yes	no
Adult females hunt during nestling period	no	yes
Growth rate (K)	0.12	0.13 (0.043, 14)[c]
$t_{10\text{-}90}$ (d)	36.7	37.2 (11.456, 14)
Mean asymptotic weight (g)	1587	1564 (195.2, 14)
Mean fledging age (d)	51.0	51.96 (3.82, 14)
Inactive time (%)	43.0 (6.2, 69)	29.9[d] (14.9, 52)
Fish delivery rate (fish/h)	0.527 (0.06, 69)	0.351[d] (0.14, 52)
Mean fish size (g)	237.1 (160, 145)	156.9[d] (167, 254)

[a] From Stinson (1976, 1977, 1978).
[b] From McLean (1986).
[c] Mean (SD, N).
[d] Denotes pairs of values that are significantly different ($P < 0.001$).

10 to 90% of the asymptotic weight was 37.23 ± 11.5 days (N = 14). Growth rates as derived above (Ricklefs 1967, 1968, 1976; Stinson 1977) reflect the rate of growth as a percentage of the asymptote. Because male and female asymptotic weights differed significantly (male: 1365 ± 90.62 g, N = 5, female: 1645 ± 148.6 g, N = 5, $P = 0.007$), and because both sexes took about the same time to fledge (male: 51.0 ± 5.3 days, N = 5, female: 50.6 ± 2.9 days, N = 5; $P = 0.886$) the absolute rate of growth must be higher for females.

Examination among and within broods revealed a disparity in growth and fledging times between dominant and subordinate young. Among broods, the young of Nests 5, 6, and 7 took significantly longer to fledge than the young in some of the other nests. Within-brood comparisons showed that the lighter young of Broods 5 and 7 took significantly longer to fledge (57.5 ± 3.5 days, N = 2, $P = 0.017$) than the other young (50.9 ± 3.1 days, N = 12). Also, the lighter young (male) of Brood 5 was at least six days older than the other males at the last weighing before fledging, yet it had the lowest asymptotic weight and the shortest body length (43.2 cm) of all other Osprey young (mean = 50.1 cm).

Nestling deaths occurred in two of the seven broods. One of the chicks died at approximately six days of age and another was 10 days old at death. Both bodies were found in their nests, with little evidence of external injury. Necropsies performed by a local veterinarian indicated malnutrition as the probable cause of death.

Discussion.—Sibling aggression in 1985 was common among nestling Ospreys in southwestern Chesapeake Bay. Roberts (1982) documented aggression between siblings of two nests in the bay. In one case, the adults abandoned two young, 18 and 19 days old (Roberts, pers. comm.). Spitzer (unpubl. data) has monitored Osprey productivity in several areas of the bay's eastern shore and has noted brood reduction in approximately 75% of the nests in at least one area. However, there have been no published reports of sibling aggression or

brood reduction among Chesapeake Bay Ospreys. In fact, Stinson (1976, 1977) found no signs of sibling aggression during his 1975 study of the reproductive behavior of Ospreys inhabiting the western shore of the bay. The adult Ospreys appeared to feed all young, and crops that were examined were never empty (Stinson 1976). In 1985, we observed 32 sibling attacks, and threatening postures and kleptoparasitism among siblings were common. Typically, more than half of the nestlings' crops were empty during our visits. In 1975, the young were fed sequentially (Stinson 1976). In 1985, in many instances, the young dominated each other through aggression and/or posturing and, as a consequence, feeding of the young was often nonsequential. Heavier young were fed repeatedly and lighter young were often ignored.

In 1985, the amount of time the male spent perched near the nest and the delivery of fish to the nest significantly decreased compared to 10 years earlier (Table 1). In 1975, the males spent about 43% of the day near the nest (Stinson 1976) in contrast to less than 30% in 1985. The delivery rate significantly declined from over 0.5 fish/hour in 1975 (Stinson 1976) to about 0.3 fish/hour in 1985. Also, the average size of the fish delivered to the nest was significantly greater in 1975 than in 1985. In 1985, Chesapeake Bay Ospreys apparently hunted more and delivered fewer fish than they did 10 years earlier.

There were several other striking differences between the data of 1975 and 1985 (Table 1). Although Stinson found the mass-rank of a chick changed from one weighing period to the next, all but one of the young studied in 1985 maintained rank consistently. In the exceptional case (Nest 7), change in rank was likely due to the sex of the young; the male's weight was exceeded by that of his two younger, female nestmates. Stinson (1977) noted that males often fed the young. In 1985, we never saw males feed young. Furthermore, none of the adult females of the 1975 study contributed to the hunting efforts until the fledgling period, as is typical of female Ospreys (Bent 1937). In 1985, one of the seven females hunted and this female began hunting three weeks into the nestling period—five weeks before the young had fledged.

In reviewing 1975 and 1985 data, the lack of a large difference in some of the values is puzzling (Table 1). If less food was being delivered in 1985 than in 1975, one might expect a lower growth rate, a lower average asymptotic weight and a greater t_{10-90} value and a greater average fledging age. We found no differences in any of these parameters. The small and unequal sample sizes in the two studies (Stinson 1977: five, one-young, one, two-young, two, three-young, one, four-young, and one, five-young broods; McLean 1986: one, one-young, five, two-young and one, three-young broods) may explain why the values are so comparable. Also, Stinson (1977) did not distinguish between sexes; the proportion of male and female young studied would affect the average asymptotic weight.

Other studies (Knight 1932, Poole 1979, Judge 1981, Jamieson et al. 1983) have noted the incidence of sibling aggression, and one report (Poole 1982) has implicated food shortage as the probable cause of sibling aggression and subsequent brood reduction. Knight (1932) noted one brief occurrence of aggression between two very young Osprey chicks. In Canada, 18 incidents of aggression were recorded during 449 h of observation of eight nests during the summers of 1978 and 1980 (Jamieson et al. 1983). There, aggression was noted to be more common later in the nestling period (when young were approximately four to five weeks old) and more prevalent in three-young than two-young broods. There appeared to be no fish shortage in the study area and the average rate of delivery of fish (0.48 fish/h) was similar to that found by Stinson (1976), but greater than the rate found in 1985. Jamieson et al. (1983) concluded that because most aggression was observed in these three-young broods, then competition for food, even if relatively abundant, results in aggression. In Florida Bay, Poole (1979) documented the constant aggression of one nestling against its nestmate. Measurements gathered in the days during and after observing the aggression

showed a significant difference in size and weight between the aggressor and the intimidated sibling—differences very similar to those we observed in Chesapeake Bay Osprey young in 1985. Poole (1982) noted that sibling aggression could be turned on and off with the degree of hunger of the dominant young, which argues that food availability does, in fact, influence this behavior. The aggressive young nearly always ceased aggression after satiation—a finding identical to ours. Hatching asynchrony, as well, might have influenced the incidence of sibling aggression and the subsequent brood reduction observed in the Florida Bay Ospreys (Poole 1982). Third chicks in food-stressed colonies grew significantly slower than their siblings (Poole 1982). In short, Poole (1979, 1982) offered evidence to suggest that sibling aggression is due to food scarcity and, to a lesser degree, hatching asynchrony. Aggression was integral to brood reduction; subordinate siblings were forced out of the nest, or, more commonly, denied access to food.

Some of our results are easily explained, but others are seemingly paradoxical. Young in Nests 5, 6, and 7 took significantly longer to fledge than the other young. This delay in fledging times coincided with a substantial amount of sibling aggression and/or brood reduction observed in these nests. These results, then, imply delayed maturation as a result of sibling aggression. Yet, at these same nests, the occupants were the recipients of the greatest amount of fish. Such a result is contrary to expectation, particularly if sibling aggression and brood reduction are associated with food scarcity.

But a closer examination within broods is revealing. Although the occupants of Nest 5 received a large amount of fish, some was left uneaten, and a disproportionate share was eaten by the adult female and the dominant young. Based on our bite-counts, the dominant young of this nest ate twice as much as the subordinate young. Because the subordinate young was intimidated from eating, begging calls from it and subsequently from the adult female appear to have resulted in more fish being delivered to the nest. Also, of all adult females of the two-young broods, this female ate proportionately more than her young (34 vs 22%). It is conceivable her energetic demands were greater than others due to a host of factors including body size, quality of feeding during courtship, or demands of egg laying (cf Poole 1985). In Nest 7, a three-young brood may have been the stimulus for more fish delivered. Indeed, the male of this nest was the most active (inactive time = 12.7%) and had the highest rate of delivery of fish (0.421 fish/h) of any adult male. The young of this nest were vocal as well, and it was our impression that the subordinate young was inordinately vocal; this young was often neglected during feeding either through intimidation by the heavier siblings or by inaccessibility to the adult female when she distributed the food. Even though a substantial amount of energy was being delivered to these nests, in at least two cases (Nests 5 and 7) the young were receiving unequal shares.

Sex of the hatchlings and hatching asynchrony appear important in facilitating aggression and brood reduction. Male and female young differ in both asymptotic weights and absolute growth rates. Females grow faster and become heavier than males. However, being hatched a day or two before a nestmate confers an advantage as well. In brood 7, the male was hatched a day before one female and two days before the other. This male was able to maintain dominance over the females even though the females eventually became heavier. The five-day difference in age of the two young of nest 6 was probably partially responsible for the death of the one at 10 days of age. This is consistent with Stinson's (1979) proposal that the predominance of siblicide in raptors is facilitated by asynchronous hatching; this usually permits the older chick to dominate the younger one.

However, the ultimate cause of sibling aggression and brood reduction is probably food shortage (O'Conner 1978, Stinson 1979, Mock 1984). Although there is a positive correlation between sibling aggression and energy delivered to the nest, such a relationship may be best explained by ultimate rather than proximate factors (Mock 1984). Mock argues that there

is no necessary relationship between the timing of sibling aggression and subsequent food shortages and that sibling aggression does not have to occur during feeding. In this study, not all of the attacks were during feeding. In fact, a number of the posturing behaviors occurred in the absence of food. Additionally, even though Broods 5, 6 and 7 received large amounts of fish, the average rate of delivery to these nests (0.424 ± 0.14 fish/h, N = 24) was still significantly less than the average rate of delivery in 1975 ($P = 0.001$, Table 1). Because the average size of fish delivered in 1985 was significantly less than that delivered in 1975 (Table 1), then obviously the males of these nests were delivering significantly less fish in 1985 than 10 years earlier.

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Intraspecific piracy in Ospreys.—Piracy is a common foraging tactic in birds. By stealing prey, pirates avoid incurring time and energy cost of locating, handling, and transporting prey but may risk injury if the owner defends the contested resource (Brockmann and Barnard 1979, Hansen 1986). Ospreys (*Pandion haliaetus*) are frequent victims of interspecific piracy (Bent 1937, Prevost 1979), since their conspicuous mode of prey transport and reduced flight agility when carrying prey make them easy targets, but intraspecific piracy is heretofore unreported.

I studied Ospreys in the Creston Valley of southeastern British Columbia particularly at a nest with two chicks on a bridge at the mouth of the Kootenay River (49°15′N, 116°41′W). On 13 July 1987, the chicks (28 and 24 days old) were nearly identical in mass (1205 vs 1180 g), and at feeding bouts that day received similar portions of food. A severe 3-day rainstorm began on 16 July, during which time no observations could be made at the rest. Strong winds and thunderstorms occurred continuously throughout this period. Nest-watches resumed on 19 July, when the storm had abated. At 1008 h the parent male delivered a black bullhead (*Ictalurus melas*) which the female fed to the chicks. Although no aggression occurred, the older chick ate 78% of the 83 bites eaten by the chicks. The younger chick appeared weakened, and by 1305 h was lying on its back making only feeble movements. At that time, the female parent left the nest and flew toward a second male from an adjacent nests which was standing on the riverbank with a live largescale sucker *Catostomus macrocheilus*; estimated mass 600 g). The female grabbed the caudal peduncle of the sucker, and a prolonged tug-of-war with the male ensued. The male resisted the female's attempts to take the fish until the female released the fish and attacked the male, biting his bill and head. The female then flew with the sucker to a site about 300 m north of the bridge. During this flight, she was attacked and struck twice by the victimized male. The male returned to its nest 300 m south of the bridge and the female ate the anterior portion of the fish over the next 31 min. At 1351 h she returned to the nest with the fish, and over the next 2 h and 27 min, at two feeding bouts, fed the older chick 544 bites. The hunger of the female

and older chick was clearly evident. The 472 bites the chick ate at the first of these feeding bouts exceeded by 26× the mean amount eaten ($\bar{x}$ = 17.8, range = 0–54 bites) at six feeding bouts immediately prior to the rainstorm (13–15 July). Similarly, the 109 bites the female ate before delivering the sucker to the nest exceeded by 8× the mean amount ($\bar{x}$ = 13.5, range = 2–57 bites) she ate at six feeding bouts on 13–15 July.

The younger chick became weaker and by 1600 h had died. At no time during these feeding bouts did the female offer it food. The carcass was recovered and was found to be severely emaciated (mass = 915 g, a decline of 265 g from 13 July). There were no indications of physical abuse, and I assume starvation was the cause of death. The older chick subsequently survived to fledge from this nest.

This case of piracy by the female Osprey apparently was not just an opportunistic theft of an unusually large prey item; large suckers were taken frequently by Ospreys from the three nests (the focal nest and two adjacent nests) at the mouth of the Kootenay River, thus she had many opportunities to steal similar prey but did not do so. Moreover, female foraging during brood-rearing is itself unusual; male Ospreys normally deliver virtually all of the prey to the family from the onset of incubation until late in the nestling period (Stinson 1978, Levenson 1979, Jamieson et al. 1982, Stinson et al. 1988).

The extreme hunger of the female and/or her chicks appears to have driven her to seek food by piracy. Presumably the food deliveries of the male during the rainstorm were insufficient to meet the food needs of the family, as Osprey hunting success may be severely depressed during heavy winds and rain (Poole 1984, 1989). I suspect that the prospect of escalated fighting (as occurred here) normally deters Ospreys from intraspecific piracy.

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Depredation of artificial avian nests in irrigated forests.—Predation is a major factor reducing avian nesting success (Ricklefs 1969). Greater vegetative density near avian nests may reduce predator foraging efficiency, thereby lowering incidences of depredation of nests (Bowman and Harris 1980, Sudgen and Beyersbergen 1986, Yahner and Cypher 1987). Further, avian predators on nests tend to predominate in forested habitats, whereas mammalian predators are more common in farmland habitats (Angelstam 1986). Our previous studies have shown that American Crows (*Corvus brachyrhynchos*) and Blue Jays (*Cyanocitta cristata*) were major predators on artificial avian nests placed in even-aged forest stands, and mammals were relatively unimportant as predators (Yahner and Voytko 1989, Yahner et al. 1989). Moreover, because corvids locate food resources via vision, arboreal nests in even-aged stands are more susceptible to disturbance than ground nests (Yahner and Scott 1988). In order to understand better long-term trends in regional populations of avifauna, more attention should be given to relationships among vegetative density near nest sites, habitat type in which nests are located, and relative abundance of predators associated with a particular habitat type (Picman 1988).

A portion of state game lands (SGL) 176, Centre County, Pennsylvania, has been irrigated with chlorinated sewage effluent (hereafter termed wastewater) since 1983 (Rollfinke et al. 1990). As a consequence of this irrigation, vegetative structure is considerably different between irrigated and nonirrigated forest stands (Rollfinke et al. 1990). The irrigated sector of SGL 176 is approximately a 50:50 intermix of forest and farmland/old field habitat types (Rollfinke et al. 1990) which likely affects the relative abundance of avian versus mammalian predators on avian nests compared to more forested sites in the region (after Angelstam 1986). Diversity and abundance of breeding birds are much higher on irrigated than nonirrigated forest stands at SGL 176, suggesting that irrigated stands are better habitats than nonirrigated stands (Rollfinke et al. 1990). However, the "quality" of irrigated stands for breeding birds cannot be assessed fully until information on productivity and survivorship is obtained (Van Horne 1983). Thus, our objective was to compare depredation of artificial ground and arboreal nests placed in forest stands irrigated with wastewater to those placed in contiguous nonirrigated stands. These findings will be valuable in assessing the impact of forest irrigation on regional bird populations.

Study area.—Our study was conducted on an irrigated and an adjacent nonirrigated forest stand at SGL 176, Centre County, Pennsylvania (hereafter both stands are referred to collectively as the Toftrees area). The irrigation system occurred on 200 ha and contained 3100 rotating sprinklers connected by a parallel network of pipes, each spaced 25 m apart. The system applied about 264 cm of wastewater annually compared to an average annual precipitation of 93 cm (Rollfinke et al. 1990).

Forest stands on the Toftrees area were approximately 50 to 60 years old and consisted principally of mixed-oak (*Quercus* spp.) and red maple (*Acer rubrum*). Major woody stems (<2.5 cm diameter) on irrigated and nonirrigated stands included red maple, black cherry (*Prunus serotina*), white sassafras (*Sassafras albidum*), and *Rosa* spp. Percent coverage of herbaceous vegetation was much greater on the irrigated (57%) than on the nonirrigated stand (5%) ($P < 0.01$). A lush herbaceous layer grew to a height of 1–2 m on the irrigated stand and was comprised principally of white snakeroot (*Eupatorium rugosum*), common pokeberry (*Phytolacca americana*), and Canada clearweed (*Pilea pumila*).

Common avian species nesting less than 2 m from ground level on the Toftrees area included Ruffed Grouse (*Bonasa umbellus*), Wood Thrush (*Hylocichla mustelina*), Ovenbird (*Seiurus aurocapillus*), Common Yellowthroat (*Geothlypis trichas*), Hooded Warbler (*Wil-*

sonia citrina), Northern Cardinal (*Cardinalis cardinalis*), Indigo Bunting (*Passerina cyanea*), and Rufous-sided Towhee (*Pipilo erythrophthalmus*) (Rollfinke et al. 1990).

Methods.—Thirty random sites each were selected on irrigated and nonirrigated stands during five time periods (trials) from May to July 1989. Minimum distance between sites was 25 m, and each site was greater than 50 m from a disturbance, such as an old field or a clearcut stand. On the irrigated stand, sites were midway between parallel pipelines. Of the 30 sites per stand during each trial, 15 were randomly selected for placement of ground nests and 15 for placement of arboreal nests.

A nest consisted of two fresh, brown chicken eggs (Yahner et al. 1989). Ground nests were placed next to the nearest stump, log, or tree in a slight depression in leaf litter (Yahner and Wright 1985); arboreal nests were put in cups (chicken wire, 10 cm × 10 cm deep), which were lined with leaf litter and attached 1.5 m above ground to the nearest woody stem (1–5 cm dbh) (Yahner and Cypher 1987).

The fate (undisturbed, disturbed by an avian predator, or disturbed by a nonavian predator) of each nest was determined five days after placement (Yahner et al. 1989). A disturbed nest had a broken or missing egg by day 5. Nest or egg appearance and mode of disturbance were used to categorize predators as avian or nonavian (Rearden 1951, Yahner and Wright 1985, Yahner and Cypher 1987). We wore rubber gloves and boots when placing nests to reduce human scent near nests. Because nests were visited only when placed, paths in vegetation were not developed by investigators. Nests, eggs, and egg fragments were removed at the end of a trial.

The influence of forest irrigation (irrigated vs nonirrigated stand), nest type (ground vs arboreal), and time period (trials 1–5) on nest fate was analyzed by 2- to 4-way tests-of-independence (BMDP4F, Dixon 1985). Likelihood ratios (G^2) were computed to test for interactions between nest fate and the three other variables using log-linear models, which is appropriate when examining attribute variables in multi-way contingency tables (Sokal and Rohlf 1981, Dixon 1985). We counted the numbers of American Crows and Blue Jays that were 200 m or less from field personnel during time of placement and removal of nests during each trial. Relative numbers of these avian predators were compared to those noted in previous studies (Yahner and Scott 1988, Yahner et al. 1989).

Results.—Of 300 nests, 237 (79%) were disturbed during the five trials (Table 1). Only five (2%) of the disturbed nests were affected by avian predators; the remaining 232 (98%) nests were likely disturbed primarily by mammalian predators, e.g., raccoons (*Procyon lotor*), based on mode of distance.

Nest fate was not associated with forest irrigation, nest type, or time period. One hundred twenty-one (81%) and 116 (77%) of the nests placed in irrigated and nonirrigated forest stands, respectively, were disturbed ($G^2 = 0.68$, df = 2, $P = 0.71$) (Table 1). One hundred twenty (80%) of the ground nests and 117 (78%) of the arboreal nests were disturbed ($G^2 = 0.37$, df = 2, $P = 0.83$). Numbers of disturbed nests per trial ranged from 42 (70%) in trial 2 to 51 (85%) in trial 5 ($G^2 = 10.95$, df = 14, $P = 0.69$). Numbers of American Crows and Blue Jays per trial averaged 5.2 (range = 3–8) and 0.4 (range = 0–1), respectively.

Discussion.—Depredation rate (79%) of nests on irrigated and nonirrigated stands combined at the Toftrees area was higher than those noted in several other studies of predation on either artificial or natural nests. For instance, our previous studies of artificial ground and arboreal nests in even-aged forest stands less than 10 km from the Toftrees area reported rates of nest disturbance by predators ranging form 31–61% (Yahner and Cypher 1987, Yahner and Scott 1988, Yahner et al. 1989). Depredation rate of natural songbird nests on these same even-aged stands over a 3-year period was 48% (Yahner, unpubl. data). Wray et al. (1982) noted that 43% of nests established by four species of grassland sparrows were lost to predators. Yahner (1982) recorded that 44% of American Robin (*Turdus migratorius*)

TABLE 1

NUMBER OF GROUND AND ARTIFICIAL NESTS DISTURBED BY PREDATORS DURING FIVE TRIALS ON AN IRRIGATED FOREST STAND AND A NONIRRIGATED FOREST STAND AT STATE GAME LANDS 176, CENTRE COUNTY, PENNSYLVANIA, 1989

Trial (dates)	Nest type[a]	Irrigated	Nonirrigated
1 (24–29 May)	Ground	12	12
	Arboreal	12	9
2 (7–12 Jun)	Ground	11	12
	Arboreal	12	7
3 (21–26 Jun)	Ground	13	13
	Arboreal	12	11
4 (5–10 Jul)	Ground	10	14
	Arboreal	13	13
5 (19–24 Jul)	Ground	12	11
	Arboreal	14	14
All trials combined	Ground	58	62
	Arboreal	63	54
	Total	121	116

[a] N = 60 nests per trial divided equally between stands and nest types (ground vs arboreal).

nests and 68% of Mourning Dove (*Zenaida macroura*) nests were lost to predators. In contrast, Best (1978) found that 76% of the nests created by Field Sparrows (*Spizella pusilla*) were preyed upon. Redmond et al. (1982) observed considerable differences in predation on nests between two races of Spruce Grouse (*Canachites canadensis*), with a 70% nest loss in *C. c. franklinii* but only a 19% loss in *C. c. canace.*

The irrigated stand at the Toftrees area contained an abundant and a diverse breeding-bird community, in part due to the ready availability of foraging sites and food resources (Rollfinke et al. 1990). However, because depredation of artificial nests was pronounced throughout the Toftrees area, both the irrigated and the proximal nonirrigated stand may be relatively low in "quality" to breeding birds (after Van Horne 1983). But data on avian productivity of natural nests at the Toftrees area would be necessary to support or refute this contention.

Depredation rate of nests at the Toftrees area was probably not influenced by lush herbaceous vegetation on the irrigated stand. Other studies have shown that avian nests were less susceptible to predation when located in dense vegetation, which either impeded foraging efficiency of predators or provided increased concealment (e.g., Bowman and Harris 1980, Yahner and Wright 1985, Sugden and Beyersbergen 1986).

In contrast to studies of depredation of artificial nests on even-aged forest stands near the Toftrees area (e.g., Yahner and Scott 1988, Yahner et al. 1989), most disturbed nests (98%) at the Toftrees area were affected by nonavian predators. Yahner and Scott (1988), for example, found that 72% of the disturbed nests in even-aged stands were attributed to avian predators. Perhaps this differential impact of mammalian vs avian predation on nests is explained partially by habitat type on the two areas. The Toftrees area contained an intermix of forest and farmland/old field cover types, whereas even-aged forest stands in the previous studies were surrounded on 95% of their boundaries by forest. Hence, the Toftrees area,

with a great percentage of farmland, might be expected to have a lower number of avian than mammalian predators (Angelstam 1986). Although numbers of American Crows at the Toftrees area were comparable to those in even-aged stands in the region (e.g., $\bar{x} = 4.8$ crows per trial, range = 2–9; Yahner et al. 1989), numbers of Blue Jays, which are considered a principal predator of avian nests (e.g., Picman 1988), were virtually absent from the Toftrees area. Yahner et al. (1989), for instance, recorded much higher numbers of Blue Jays in even-aged stands ($\bar{x} = 10.5$/trial, range = 0–12) than at the Toftrees area.

We attribute most nest predation on the Toftrees area to mammals, particularly raccoons, for three reasons. First, a comparable number of ground and arboreal nests were preyed upon. If birds were the principal predators, we would expect greater numbers of arboreal nests to be lost rather than ground nests (e.g., Yahner and Scott 1988). Raccoons are capable of climbing woody stems to reach nests, and bird eggs are an abundant and easily accessible food resource to raccoons (Greenwood 1981). Second, raccoons were the principal large mammalian predator captured on the Toftrees area (Brown 1989). Although raccoon density on our study area probably was similar to some other sites in Pennsylvania (C. L. Brown, pers. comm.), density was likely higher than on the xeric, even-aged forest stands examined in previous studies (Yahner and Scott 1988, Yahner et al. 1989). Third, a greater density of raccoons might be expected at the Toftrees area because of abundant water and food resources (see Sanderson 1987). Several small ponds formed on the irrigated stand at Toftrees area as a result of irrigation, and farm crops (e.g., corn), invertebrates, and berries were abundant (Rollfinke et al. 1990).

Because rates of depredation did not increase over time, we do not believe that raccoons or other mammalian predators were using human scent to locate nests. Further, because depredation rate did not vary among trials, we believe that predators did not learn over time to better exploit the irrigated and nonirrigated stands with artificial nests nor did they improve their ability to find nests by developing a search image for nests (Yahner and Wright 1985).

In conclusion, differences in vegetative structure resulting from forest irrigation did not affect depredation rates of artificial avian nests, at least within the immediate study area. This finding is valuable in understanding the impacts of habitat alterations on long-term trends in avian population numbers (Whitcomb et al. 1981) because application of wastewater to forest stands is expected to increase in the future as a viable means of waste disposal (Nutter and Red 1986). We concur with other investigators (e.g., Bowman and Harris 1980, Picman 1988) that comparisons of predation rates among habitats in future studies should include a consideration of the relative abundance of predators because foraging strategies are species- or taxon-specific, and hence, their impact on avian nests (ground vs arboreal) may vary on a localized scale.

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Nest-site fidelity in Red-headed and Red-bellied woodpeckers.—Numerous studies demonstrate the propensity for birds to nest at the same location in successive years (Kendeigh 1941, Werth 1948, Austin 1949, Greenwood 1980). Such nest-site fidelity may occur in either migratory (Gauthreaux 1982) or non-migratory (Harvey et al. 1979) species. Studies that substantiate this phenomenon in woodpeckers, however, are relatively few. Jackson (1978, 1987) and Hooper et al. (1980) report that Red-cockaded Woodpeckers (*Picoides borealis*) commonly use the same nest cavities in consecutive years. The Hairy Woodpecker (*P. villosus*), a species whose investment in cavity excavation is less than that of the Red-cockaded Woodpecker, also often returns to the same nest tree (Kilham 1960). Among migratory species, the Northern Flicker (*Colaptes auratus*) and the Yellow-bellied Sapsucker (*Sphyrapicus varius*) exhibit nest-site tenacity (Lawrence 1967). The extent to which Red-headed and Red-bellied woodpeckers (*Melanerpes erythrocephalus* and *M. carolinus*) return to previous nest sites is unclear. Short (1982) suggests that resident Red-headed Woodpeckers may use previously excavated winter roost holes as nests, but mentions nothing of whether migratory individuals return to nest in previously occupied trees. Bent (1939) reports that Red-bellied Woodpeckers often excavate nests in limbs used during a previous year and occasionally nest in the same cavity. The potential effects of European Starling (*Sturnus vulgaris*) competition on woodpecker nest-site fidelity and the extent to which reproductively successful Red-headed and Red-bellied woodpeckers return to previous nest sites is equally ambiguous. Thus, the three objectives of this study were to determine: (1) if either Red-headed or Red-bellied woodpeckers reuse old nest cavities or nest in the same tree or immediate area during consecutive years, (2) whether nest-site fidelity is influenced by the previous reproductive success of returning individuals, and (3) whether starling competition for nest cavities influences whether or not Red-headed or Red-bellied woodpeckers return to previous nest sites.

Methods.—From mid-July 1984 through August 1987, adult and juvenile Red-headed and Red-bellied woodpeckers were captured on the Mississippi State Univ. (MSU) campus, the MSU south farm, and in the city of Starkville, in Oktibbeha County, Mississippi. Most frequently, nestlings were taken from nests with the use of a noose (cf. Jackson 1977). Adult birds were captured on nests using a pole equipped with a net on the end. Adult and juvenile woodpeckers were captured away from the nest with the use of a mist net, recordings of woodpecker distress calls, and plastic decoys. Each captured woodpecker was fitted with a U.S. Fish and Wildlife Service aluminum band and a unique color-band combination to permit individual recognition.

To determine the extent to which Red-headed and Red-bellied woodpeckers returned to previous nest sites, I visited such locations in subsequent breeding seasons in search of active nests. If color-banded nesting woodpeckers were not detected in the same tree or immediate area (circular plot of 400 m^2; radius = 11.3 m), I thoroughly searched a circular plot of approximately one ha around the cavity tree. In addition, I explored new areas in the last three years for other nesting woodpeckers. All observations were made with either a 15–45 zoom spotting scope or 7 × 35 binoculars.

Results.—Of 114 Red-headed Woodpeckers color-banded during this study, 45 were banded as adults and 69 as nestlings. No individuals banded as nestlings returned to nest in subsequent years in the same 1-ha circular plot around the cavity tree. Of the 45 adults (all of which nested in areas of starling overlap), 15 returned to nest in the same tree or immediate area (Table 1). The Chi-square test revealed that significantly more Red-headed Woodpeckers returned than would have been expected assuming that individuals were not

TABLE 1

NEST-SITE FIDELITY OF RED-HEADED WOODPECKER IN 1984–1987 BASED ON 15 COLOR-BANDED ADULT INDIVIDUALS. A = MALE THAT RETURNED TO A PREVIOUS NEST SITE, B = FEMALE THAT RETURNED, C = MATED PAIR THAT RETURNED, AND D = INDIVIDUAL OF UNKNOWN SEX THAT RETURNED

Number of years returned	Same cavity	Same tree	Same 400-m² plot	Same one-ha plot
1	A, C	A (5)[a], B	A, D	A (2), D
2	—	A (2)	—	—

[a] Two of these individuals returned to nest in the same one-ha plot in the year prior to the two-year sequence of nesting in the same tree. A third individual nested in the same one-ha plot in the year following the two-year sequence of nesting in the same tree.

nest-site tenacious ($\chi^2 = 50$, $P < 0.001$, df = 3). In two instances, banded woodpeckers returned to nest in the same cavity during consecutive years. In six additional instances, either the male or female returned to nest in the same tree during two consecutive years, and in two cases, males returned to nest in the same tree during three consecutive years (Table 1). To a lesser extent I observed adult Red-headed Woodpeckers return to nest in other trees within the same 400 m² or one-ha circular plot around the cavity tree in consecutive years (Table 1).

All returning banded Red-headed Woodpeckers had been successful at fledging at least one young during the previous year. Five pairs with at least one color-banded individual successfully reared two broods in one year and a single brood in the other. Five other pairs raised one brood in each of two years. However, at six locations, banded individuals that fledged at least one young did not return to nest in the same area (one-ha circular plot) the following year (at two of these locations the cavity tree was cut down between nesting seasons).

All returning banded Red-headed Woodpeckers nested in areas of starling overlap, although competition for cavities between the two species was minimal (cf. Ingold 1989). Only one pair lost its cavity to starlings. At three locations, pairs with at least one color-marked individual nested concomitantly with starlings in the same tree or pole for two consecutive years (cf. Ingold 1990). One additional pair returned to nest in a tree after having nested simultaneously with starlings in the same tree during the previous year.

Sixty-seven Red-bellied Woodpeckers were color banded during this study. Sixty-one

TABLE 2

NEST-SITE FIDELITY OF RED-BELLIED WOODPECKERS IN 1984–1987 BASED ON FIVE COLOR-BANDED ADULT MALES (A)

Number of years returned	Same cavity	Same tree	Same 400-m² plot	Same one-ha plot
1	—	A[a]	—	A (2)
2	—	A	A	—

[a] This male nested in the same one-ha circular plot in the year prior to the two-year sequence of nesting in the same tree.

individuals were banded as nestlings, while only six birds were banded as adults. Red-bellied Woodpeckers in this study were less aggressive than Red-headed Woodpeckers (cf. Ingold 1989) and were difficult to lure into a mist net. In addition, the height and angle of many Red-bellied Woodpecker cavity entrances made it difficult to capture adults on the nest. Of the 61 Red-bellied Woodpeckers banded as nestlings, I detected none that returned to nest within a 400-m^2 circular plot around the cavity tree in which they were reared. However, I located two individuals that nested in the same one-ha circular plot in which they were reared at least two years after they were banded. Of the six individuals banded as adults, five returned to nest in the same tree or immediate area (Table 2). A Chi-square test revealed that significantly more Red-bellied Woodpeckers returned than would have been expected assuming that individuals were not nest-site tenacious ($\chi^2 = 8.67$, $P < 0.05$, df = 3). Two of these individuals nested in the same tree for two and three consecutive years, respectively. A third male nested within the same 400-m^2 area for three consecutive years, while two additional males nested in the same one-ha circular plot for two consecutive years (Table 2).

Four of five Red-bellied Woodpecker pairs in which color-banded males returned to the same nest sites were exposed to starling competition. Three of these pairs lost freshly excavated cavities to starlings in two consecutive years. Two of these three pairs fledged young from single nest efforts after starlings were no longer starting nests in at least one of the two years. A fourth pair, exposed to both starling and Red-headed Woodpecker harassment (cf. Ingold 1990), fledged young from at least one brood in each of two years. This particular Red-bellied Woodpecker pair nested simultaneously in the same tree with Red-headed Woodpeckers during the second year (Ingold 1990). The single Red-bellied Woodpecker pair not exposed to starling or Red-headed Woodpecker competition successfully raised two broods in each of the first two years, but lost its brood to a gray rat snake (*Elaphe obsoleta spiloides*) in the third year.

Discussion.—One of the selective advantages of nest-site fidelity in birds is that they undoubtedly have an increased and continuing familiarity with local conditions, thus potentially enhancing their reproductive success (Freer 1979, Gavin and Bollinger 1988). My observations of banded woodpeckers suggest that both Red-headed (migratory or semi-migratory) and Red-bellied woodpeckers (resident) often return to nest at specific locations during consecutive years. Nest-site fidelity in Red-headed Woodpeckers appears strong. Red-headed Woodpeckers returned to nest in the same tree, snag, or utility pole during consecutive years more frequently than did Red-bellied Woodpeckers. This may have been due in part to the likelihood that the availability of snags and old poles (in which Red-headed Woodpeckers tend to nest) is limited relative to the availability of dying branches in healthy trees (in which Red-bellied Woodpeckers often nest) (cf. Ingold 1989). In addition, such snags and poles in open areas are more likely to dry out faster and decay more slowly, thus making them habitable for a longer time.

All of the Red-headed Woodpeckers that returned to either the same tree, pole, or one-ha circular plot around such a tree or pole, and 80% of the Red-bellied Woodpeckers that returned, fledged at least one young during the previous year. The results of several studies show that reproductively successful birds (those that fledged at least one young) in a variety of altricial, migratory species tend to return to previous successful breeding locations more often than unsuccessful ones (Shields 1984, Blancher and Robertson 1985, Gavin and Bollinger 1988). Exposure to starling competition during a previous breeding season appeared to have little effect on whether or not individuals of either species returned. Red-headed Woodpeckers experienced minimal starling competition for cavities (cf. Ingold 1989), and all nest-site tenacious pairs had been successful at fledging at least one young during the previous year. However, not all reproductively successful Red-headed Woodpeckers

returned to old nest sites. Herein lies an inherent problem in nest-site fidelity studies most applicable to those with larger sample sizes (cf. Gavin and Bollinger 1988). How does one distinguish between winter bird mortality and an apparent lack of nest-site fidelity? Red-headeds that were successful at fledging young at given locations appeared to have been influenced by their success when deciding whether or not to return. However, it is difficult to speculate on the extent to which unsuccessful birds failed to return because they were unsuccessful. In addition, because most banded Red-headed Woodpeckers I observed were males, I could not determine the potential effects that sex may have had on Red-headed Woodpecker nest-site fidelity.

Although Red-bellied Woodpeckers observed in this study were exposed to extensive starling competition for nest sites (cf. Ingold 1989), they often returned to nest in the same tree or 400-m^2 circular plot during consecutive years. Twice, male Red-bellied Woodpeckers returned to previous nest sites despite each having lost at least one nest cavity to starlings during the previous season. Although each pair was forced to forego two nesting efforts early in the season, they were both successful in fledging at least one young later in the season. These data suggest that Red-bellied Woodpeckers that are able to fledge at least one young during a given season, regardless of the intensity of starling harassment, may return to the same site the following season. Unfortunately, due to the small sample size of color-banded adult Red-bellied Woodpeckers, I was unable to adequately examine the extent to which unsuccessful nesters showed nest-site tenacity.

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Yellow-bellied Sapsuckers feeding at Red-cockaded Woodpecker resin wells.—Yellow-bellied Sapsuckers (*Sphyrapicus varius*) excavate rows of holes into the cambium of various tree species and feed on the exuded sap (Kilham 1956, Tate 1973). Several other species including Red-bellied Woodpecker (*Melanerpes carolinus*), White-breasted Nuthatch (*Sitta carolinensis*), Tufted Titmouse (*Parus bicolor*), and Ruby-throated Hummingbird (*Archilochus colubris*) have been observed feeding at sapsucker excavations (e.g., Foster and Tate 1966; Kilham 1953, 1958, 1983; Southwick and Southwick 1980). We have observed typical sapsucker feeding excavations in longleaf (*Pinus palustris*), loblolly (*P. taeda*), and shortleaf (*P. echinata*) pines near Red-cockaded Woodpecker cavity trees. Red-cockaded Woodpeckers (*Picoides borealis*) consistently excavate resin wells adjacent to their roost and nest cavities (Ligon 1970, Dennis 1971). The resin exuded from these wells is an effective barrier against predation by rat snakes of the genus *Elaphe* (Rudolph et al. 1990). To our knowledge there are no published observations of Red-cockaded Woodpeckers or other avian species feeding on the exudates of these resin wells. However, we have observed Red-cockaded Woodpeckers removing drops of resin from cavity entrances and their immediate vicinity on numerous occasions. Resin drops were either released with a rapid flick of the head or wiped on bark surfaces, often on an adjacent tree.

Twice we have observed interactions between resident Red-cockaded Woodpeckers and wintering Yellow-bellied Sapsuckers that focused on the Red-cockaded Woodpecker roost cavity and the associated resin wells. At 10:15 EST on 27 October 89, a male sapsucker landed at the entrance of a Red-cockaded Woodpecker's roost cavity in a longleaf pine. The

male Red-cockaded Woodpecker flew from an adjacent tree and displaced the sapsucker. The Red-cockaded Woodpecker then entered the roost cavity and remained for 8 min. During this period the sapsucker returned to the cavity tree twice and fed at the resin wells 0.5–3.0 m from the cavity entrance. The Red-cockaded Woodpecker intently watched the sapsucker during this period. Approximately 2 min after the sapsucker left the cavity tree and flew approximately 50 m to another tree, the Red-cockaded Woodpecker emerged and began foraging on an adjacent pine. The sapsucker returned to the cavity tree 3 min later and resumed feeding at the resin wells. The Red-cockaded Woodpecker immediately returned and entered the roost cavity. The Red-cockaded Woodpecker remained in the cavity approximately 2 min before emerging and aggressively chasing the sapsucker from the area.

At 09:20 on 29 January 90 a male Red-cockaded Woodpecker returned to his roost tree in a loblolly pine to find a sapsucker (sex unknown) feeding at the resin wells. The Red-cockaded Woodpecker vocalized briefly and chased the sapsucker from the area.

Roost cavities are a critical resource for Red-cockaded Woodpeckers (Copeyon et al., unpubl. data), and as such are defended vigorously. On numerous other occasions during our observations of Red-cockaded Woodpeckers, we have observed them aggressively chasing Yellow-bellied Sapsuckers from the vicinity of Red-cockaded Woodpecker cavity trees. Occasionally, the sapsuckers would return after several minutes only to be repeatedly chased by Red-cockaded Woodpeckers.

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Classical polyandry in the West Indian Woodpecker on Abaco, Bahamas.—Oring (1986) divides avian polyandry into two general types, classical and cooperative. In cooperative polyandry, groups of cooperating males share a single breeding female. Cooperative polyandry has been confirmed for the Acorn Woodpecker (*Melanerpes formicivorus*) (e.g., Mumme et al. 1983, Koenig et al. 1984, Oring 1986). In classical polyandry, individual males breed solitarily, while females divide their attention among males. We here report a case of classical polyandry in the West Indian Woodpecker (*M. superciliaris*).

Study area and methods.—From 10 May to 4 August 1988 and 13 May to 25 June 1989, West Indian Woodpeckers were observed on Abaco, Bahamas. Birds were observed in Marsh Harbour, Dundas Town, Bahama Palm Shores, Casuarina Point, Little Harbour, Snake Cay, and the pine forest south of Bahama Palm Shores. The interior vegetation of the islands consists mainly of large stands of Caribbean pine (*Pinus caribaea*); in settlements the dominant vegetation consists of coconut palms (*Cocos nucifera*) and other introduced tropical trees.

All adult birds referred to in this study were captured on the nest and color banded for individual identification. Observations were made about 10 m from the nest using binoculars. Willimont was at the study site during the summers of 1988 and 1989, and the Jacksons were there from 18 to 25 June 1988.

Results and discussion.—One color-banded female was observed at three nest sites with two different males during the 1988 season (no polyandry was observed during the 1989 season). Four nesting attempts involving this female occurred during the 1988 breeding season (Fig. 1). The female was actively involved at two nests through most of the season, and at one point was involved at three nests. The three nest sites were in dead coconut palms in residential areas of Marsh Harbour. Nest A was 5.5 m high in a 7 m palm, DBH 23 cm. Nest A2 was 2.5 m high in a 4 m palm, DBH 25 cm. Nest B was 3 m high in a 5 m palm, DBH 26 cm

The female shared incubation at nest A with color-banded male 1 while male 2 was excavating at nest B approximately 0.7 km away. Initially, both adults helped feed the chicks at nest A. By 26 May, only male 1 was observed feeding the chicks and the female was observed at nest B with male 2. On 15 June, two days after the chicks from nest A fledged, the chicks in nest B hatched. Both male 2 and the female fed chicks at nest B, although the female contributed approximately ½ as many (25 of 76) feeding trips as the male. While male 1 was feeding chicks at nest A, the female was incubating at nest B and also excavating at nest A2 approximately 50 m from nest A. Incubation at nest A2 began on 10 June, five days before the chicks hatched at nest B. During this time the female incubated at both nests. Nest A2 failed on 21 June, the day the first chick hatched. On 23 June the female and male 1 were observed mutually tapping at nest cavity A, thus re-establishing the pairbond (Kilham 1958). Renewed excavation by male 1 began at cavity A while the female was feeding chicks at nest B. On 13 July, male 2 was killed, presumably by a cat, and the female took over the feeding of the chicks. The chicks at nest B fledged on 14 July. On 19 July the female was again at cavity A with male 1. Incubation began shortly thereafter, and their chicks hatched on 4 August.

From 30 July to 4 August (when observations ended), an unbanded male excavated in nest cavity B. During this time the polyandrous female was not observed near this nest.

Polyandry allows the female to produce multiple clutches (Emlen and Oring 1977). In the case described above, the female successfully increased her reproductive success relative to other female West Indian Woodpeckers studied. Of 28 pairs observed during 1988, only

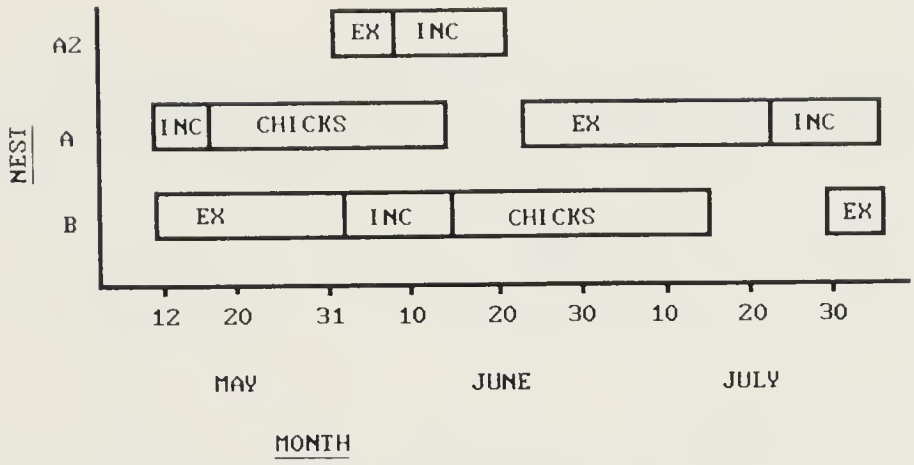

FIG. 1. Nesting phenology of a color-banded female West Indian Woodpecker at Marsh Harbour, Abaco, Bahamas. EX = excavation, INC = incubation.

five were known to have more than one brood, including the polyandrous female. It is possible that other pairs also had more than one brood or were polyandrous. However, we cannot be certain of this since we were not able to follow them throughout the entire breeding season. During 1989, 29 pairs were observed. No polyandry was noted among these pairs, but it was not possible to follow them throughout the entire breeding season or even to second broods. The polyandrous female successfully fledged two nests in 1988 (one with four chicks, the second with at least two chicks) and had chicks in a third nest when the study ended. The breeding season on Abaco appears to be long enough for two but not three broods. Polyandry may be a strategy for overcoming this limitation.

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Nest-site selection by the Herald Petrel and White-tailed Tropicbird on Round Island, Indian Ocean.—Nest-site selection is an important aspect of fitness affecting the survival of incubating adults and their reproductive success. Thermal stress is a major problem for seabirds on tropical oceanic islands (Salzman 1982). The adaptation for burrow nesting found in many species of Procellariidae protects from both predators and thermal stress, and is found in both temperate and tropical zone species. Unlike most Procellariids, however, the Herald Petrel (*Pterodroma arminjoniana*) is a surface nester. We examined its nest-site selection in comparison with that of nearby White-tailed Tropicbirds (*Phaethon lepturus*) on Round Island, 20 km north of Mauritius, in the western Indian Ocean.

Since this nearly predator-free island is largely devoid of vegetation, and the flat rocky surfaces radiate heat intensely (Gill et al. 1970), we hypothesized that birds nesting there would select sites to avoid both direct solar radiation and re-radiation. Re-radiation must be considered a major factor in evaluating heat load (e.g., Dawson 1972). Gill et al. (1970) remarked on the consistent placement of petrel nests on Round Island to maximize midday shade.

Additional factors affecting nest-site selection include competition and predation. Competition for nest sites is expected to be severe where available sites are limited, and where severe selection factors (such as predation or thermal stress) affect reproductive outcome (see references in Cody 1985). Seabirds nest on remote islands partly to escape mammalian predation. Small islands may not have sufficient food to maintain a predator's population outside of the seabird breeding season (Lack 1968). Exceptions occur, however, where there are introduced predators such as rats (Grant et al. 1981, Moors and Atkinson 1984). Island-nesting seabirds, however, are exposed to avian predators, some which are non-breeding visitors, and others which nest on the same island or on nearby mainlands.

The Herald Petrel of the Pacific and the South Trinidad Petrel of the Atlantic have been treated as separate species, *Pterodroma heraldica* and *P. arminjoniana,* respectively, but current taxonomic treatment (American Ornithologists' Union 1983), considers them subspecies. The colloquial name Herald has been applied while *arminjoniana* has priority as the specific name (Gochfeld et al. 1988). The Herald Petrel (including the South Trinidad Petrel) occurs at tropical and subtropical latitudes in the Atlantic, Indian and Pacific Oceans. The Indian Ocean population breeds only on Round Island. Based on plumage pattern and measurements, which are similar to the birds of South Trinidad Island, the Round Island petrels are referred to the nominate subspecies. Its presence as an Indian Ocean breeder was discovered only in 1949 from three specimens sent to Murphy (Murphy and Pennoyer 1952). Nonetheless, at least in October and November, the species is conspicuous at Round Island, one or more individuals being almost always in evidence wheeling over the rocky slopes where it nests.

There is a considerable literature on nest sites of petrels, including underground burrows (Brooke 1978, Byrd et al. 1983, Floyd and Swanson 1983, Schramm 1983), rock cavities, crevices, and fissures (Maher 1962, Teixeira and Moore 1983) or both (Warham et al. 1977, Boersma et al. 1980), but there is little information on the Herald Petrel. Murphy (1915) visited, but did not land on South Trinidad(e) in April 1913, and saw them "nidificating or perhaps only resting, in water-worn cells of the rock." Mathews (1936) emphasized the surface-nesting behavior of this and several other petrels and suggested it as a subgeneric character. Gill et al. (1970) described and illustrated the nesting behavior of *P. arminjoniana* on Round Island, finding only surface-nesting birds, and noted that nests were always sheltered from the midday sun either by plants or overhanging rocks. King (1984) reports a breeding range extension to Australia but provided few details on nesting.

The previously published descriptions of Herald Petrel nest sites do not compare these with unused but available habitat. In this paper, we compare the nest sites of a small subcolony of petrels on Round Island with nearby unused sites and with those used by White-tailed Tropicbirds nesting among them. We visited Round Island on 3 November 1989 and made our observations in the middle of the day when solar radiation was the most extreme. Round Island (150 ha) is a volcanic rock with a maximum elevation of 262 m. The island is predominantly smooth fissured rock with limited areas of soil suitable for burrowing species. Prior to elimination of goats and rabbits, the island vegetation was virtually destroyed, but there has been substantial recovery in recent years. Further description of Round Island can be found in Gill et al. (1970).

Round Island supports nesting Wedge-tailed Shearwaters (*Puffinus pacificus*), White-tailed and Red-tailed tropicbirds (*Phaethon rubricauda*) as well as Herald Petrels. Nearby Serpent Island supports a large colony of terns and boobies, but these have never been found nesting on Round Island. The Wedge-tailed Shearwaters excavate nest burrows in the soil areas of the island, whereas the other species nest in the rocky habitat. A nest survey in September 1989 found about 75 petrel nests and estimated as many as 150 for the island as a whole (C. Taylor, pers. comm.). Gill et al. (1970) estimated a maximum of 75 pairs of petrels on Round Island in October 1964. They provide evidence that the birds nest throughout the year, hence the Indian Ocean population may be 3–4 times that found on the island at any one time. To avoid undue disturbance to this rare bird, we examined only one typical subcolony.

The subcolony we examined had 16 nests of Herald Petrel and six nests of White-tailed Tropicbird, and encompassed a 15 × 50 m area, about two thirds of the way up the southwest slope of the island, just below and to the south of the subcolony described by Gill et al. (1970, p. 517). The area was mostly barren with one palm tree and scattered clumps of grass. The overall slope was 30–35°. The petrels nested only in rock cavities with overhanging rock, so we recorded characteristics at the nests and at the closest cavity that was at least 1 m away (assuming they might not tolerate a neighbor that was too close). We also recorded characteristics at the White-tailed Tropicbird nests and at matched cavities for these nests as well. Characteristics recorded at each cavity included contents, height, width, and depth of cavity, percent of rock cover over incubating adult or cavity, percent grass within 0.5 m in front of the cavity, depth of the shade (how much of the floor of the cavity was shaded, measured from back wall to edge of shadow), and percent of floor of cavity that was shaded. Fourteen petrel nests contained eggs, one had a young pale grey downy chick, and one was empty. Usually, the incubating adults did not move while we measured the cavity and photographed the nest site. We used Mann Whitney *U*-tests to contrast differences between nests and unused cavities.

In all cases, as mentioned by Gill et al. (1970), the petrels and tropicbirds were completely shaded from the sun at midday and were often partially protected by grass that provided additional shade. Usually, the petrels were incubating their egg, although two birds merely sat beside them. Inter-nest distance between petrels ranged from 2.2 to 10 m, and petrels on adjacent nests could not see their neighbors. Characteristics of nest cavities and unused cavities are shown on Table 1.

We contrasted the cavity size, vegetation, and shade characteristics at the 16 petrel nests with those of the unoccupied cavity nearest each nest (Table 1). We recognize that some of these unoccupied cavities might be occupied at other times. Rock cover around the cavity did not differ for nests and control sites, nor did the height or width of the cavities. Petrel nests were in deeper cavities (35 vs 15 cm), and accordingly there was more shade within 50 cm of the egg, as well as a greater depth of shade on the cavity floor. These measurements were made between 11:45 and 13:30, taking advantage of essentially noon conditions.

TABLE 1

CAVITY CHARACTERISTICS FOR NESTS OF THE HERALD PETREL AND WHITE-TAILED TROPICBIRD ON ROUND ISLAND, MAURITIUS

	Herald Petrel		White-tailed Tropicbird		Interspecies comparison
	Controls	Nests	Controls	Nests	
Rock cover	14.2 ± 22.4 5 $U = 87$	10.8 ± 10.6 10 ns	19.7 ± 21.7 11 $U = 17$	10.5 ± 8.4 13 ns	$U = 47$ ns
Cavity height	29.8 ± 17.4 27 $U = 122$	31.4 ± 11.0 29.5 ns	52.7 ± 43.7 44 $U = 18$	55.2 ± 7.8 59.5 ns	$U = 6$ $P < 0.002$
Width	53.8 ± 35.3 42 $U = 102$	54.0 ± 13.9 55.5 ns	48.7 ± 37.5 45 $U = 18$	46.8 ± 9.4 48.5 ns	$U = 33$ ns
Depth	15.1 ± 10.4 13 $U = 68$	35.4 ± 13.0 32.5 $P < 0.05$	11.8 ± 6.2 13.5 $U = 0$	38.7 ± 7.0 38.5 $P < 0.001$	$U = 31$ ns
Percent shade	32.8 ± 28.9 25 $U = 75$	53.9 ± 16.5 55 $P < 0.05$	8.2 ± 10.3 4.5 $U = 0$	74.0 ± 15.4 80 $P < 0.001$	$U = 18$ $P < 0.05$
Percent grass	4.4 ± 9.8 0 $U = 4$	29.7 ± 22.0 30 $P < 0.0001$	0.8 ± 1.9 0 $U = 0$	37.7 ± 18.1 39 $P < 0.001$	$U = 37$ ns
Shade depth	9.4 ± 9.4 7 $U = 6$	25.2 ± 9.7 25.5 $P < 0.001$	6.7 ± 6.2 5.5 $U = 0$	32.8 ± 5.5 34 $P < 0.001$	$U = 20$ $P < 0.05$
Number	16	16	6	6	

For each variable, the first line gives the mean ± SD, the second line median, and the third line the Mann-Whitney U score and its associated probability comparing nests versus controls for each variable for each species.

Cavities occupied by petrels had significantly more vegetation around the entrance than did control sites perhaps because over time the soil is fertilized by droppings from the chicks.

The six tropicbird nests found in the vicinity of the petrel cluster were examined for comparison. The same comparisons held for the tropicbirds. Their nests did not differ from controls in the amount of rock cover or in the height and width of the cavity, but they occupied significantly deeper cavities that cast more shade. Moreover, they had extensive vegetative cover at the mouth of their nest cavities, such that in some cases the incubating bird was nearly completely hidden from view.

Comparing the tropicbird nest cavities with those of the smaller petrel revealed no difference in the width or depth of their cavities, but tropicbirds preferred higher cavities ($P < 0.002$) with significantly more shade ($P < 0.05$, Table 1).

The significant differences we found between petrel nests and unused cavities seemed to reflect thermal constraints. Petrel nests were always in cavities that were deep enough to cover them, had large enough rock overhangs to provide shade at midday, and had some vegetation that would provide additional shade in the afternoon. Thermoregulation is an

important consideration for a variety of seabirds on oceanic islands (Howell and Bartholomew 1961).

Moreover, all petrel nest cavities faced downward toward the sea which would allow updrafts of cooling winds, while facilitating rapid departure from the nest. The depth of shade on the floor of the cavity is probably a significant factor which reduces the re-radiation received by the incubating bird and later its chick. Tropicbirds also selected cavities that were large and shaded at midday. The tropicbirds were located in higher (but not wider or deeper) cavities than the petrels. Prys-Jones (1980) reported that White-tailed Tropicbirds on Aldabra selected nest sites that were partly concealed from above, and 96% were enclosed by rock, in contrast to Red-tailed Tropicbirds for which 88% of the nests had only vegetative cover. At Culebra, Puerto Rico, we have seen White-tailed Tropicbirds nesting in small rocky caves, crevices, and tunnels, all nearly enclosed by rock. By contrast, Gill et al. (1970) reported Red-tailed Tropicbirds nesting in cavities similar to those of petrels and White-tailed Tropicbirds nesting in vegetation. Phillips (1987) reported that 80% of all White-tailed Tropicbird nests on Cousin Island, Seychelles, were in shallow caves and cavities or in the shade of rock overhangs and boulders. The sites we studied at Round Island were similar to those on the Seychelles, and it appears that it is concealment and protection, rather than the choice of rock or vegetation per se, which is characteristic of White-tailed Tropicbirds.

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Tristan Thrushes kill adult White-bellied Storm-Petrels.—The Tristan Thrush (*Nesocichla eremita*) is restricted to the Tristan da Cunha group of islands in the central South Atlantic Ocean. It has a catholic diet, taking a range of invertebrates and fruits, and scavenging carrion from dead birds and fishes (Hagen 1952, Richardson 1984). The species has several structural adaptations to life on oceanic islands, including fairly small, rounded wings, a reduced sternum, and robust legs and feet. These adaptations are associated with its more cursorial life-style and reduced flight capabilities compared to most members of the Turdidae. However. the most distinctive feature of the Tristan Thrush is its concave, brush-tipped tongue (Lowe 1923) that is used to extract the contents of eggs. Tristan Thrushes use their large, strong bills to make holes in seabird eggs which are a seasonally abundant resource at the Tristan islands. Tristan Thrushes also kill and eat nestlings of other landbirds on the islands, including the buntings *Nesospiza* spp. and the Inaccessible Island Rail (*Atlantisia rogersi*) (Collar and Stuart, 1985, pers. obs.). However, there are no reports of Tristan Thrushes killing fully grown birds.

We visited Inaccessible Island for four months between October 1989 and March 1990. During this period, Tristan Thrushes were seen to attack and kill fully grown White-bellied

Storm-Petrels (*Fregatta grallaria*). On two occasions, thrushes were observed perched on top of a storm-petrel, using their feet to hold down the petrel at the base of its wings and hammering at the back of the petrel's head. One of the storm-petrels, caught near the western edge of the island plateau, escaped by catching a strong updraft after shrugging off the thrush. However, the other storm-petrel was caught in dense vegetation in the center of the plateau and could not escape. It was barely alive when found.

The thrushes had exposed both storm-petrels' skulls but were not seen to penetrate the skull. However, one of three White-bellied Storm-Petrel carcasses found showing evidence of thrush predation had a caved-in skull. Storm-petrels killed by Tristan Thrushes could be distinguished from those killed by Subantarctic Skuas (*Catharacta antarctica*), the only other species that preys upon birds at Inaccessible Island (Fraser 1984, Ryan and Moloney, in press), because thrushes attacked the dorsal surface, whereas skuas either swallowed storm-petrels whole or opened them ventrally to remove the pectoral muscles (pers. obs.). Tristan Thrushes had difficulty feeding from storm-petrels they killed. Only the brains had been eaten from the storm-petrel with the caved-in skull. The head and neck had been skinned and one eye removed from another storm-petrel. The abdominal cavity of one storm-petrel was opened through a hole between the scapulars, whence the entrails had been pulled. All storm-petrels killed had fully ossified skeletons, because the observations took place during the early part of the breeding season, prior to fledging.

Some of the White-bellied Storm-Petrels killed were caught directly by thrushes. Tristan Thrushes were seen chasing storm-petrels flying over the island plateau on three occasions during the day. These pursuits took place in level flight, in the open, and 2–5 m above the ground. The thrushes flew at approximately the same speed as the storm-petrels, but the outcomes of chases were not determined because the birds flew out of sight. Tristan Thrushes may also benefit from hunting attempts by Subantarctic Skuas. Skuas chase White-bellied Storm-Petrels that venture over the island during the day, sometimes causing them to seek refuge in dense vegetation. Once among such vegetation, a storm-petrel's mobility is reduced, making it easy prey for thrushes.

White-faced Storm-Petrels (*Pelagodroma marina*) also breed at Inaccessible Island, but we found no evidence of them being killed by thrushes, probably because they only visit the island at night. In addition to killing adult White-bellied Storm-Petrels, Tristan Thrushes were seen to attack fledgling Tristan (*Neospiza acunhae*) and Wilkins' buntings (*N. wilkinsi*) at Inaccessible Island. Fledglings five- to eight-weeks old were grappled in mid-air by thrushes but managed to escape. However, a banded Tristan Bunting chick was killed by a thrush on the day it left the nest.

White-bellied Storm-Petrels (mean mass ca 53 g) are more than half the mass of Tristan Thrushes (mean mass ca 91 g), and are approximately the same total length. Other thrushes occasionally kill young birds (e.g., the Mistle Thrush [*Turdus viscivorus*] Cramp 1988), but this apparently is the first record of any thrush regularly killing birds with fully ossified skeletons. This unusual predatory behavior by Tristan Thrushes is yet another example of opportunistic niche expansion by terrestrial birds at oceanic islands.

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Behavioral ecology of Red-backed Hawks in central Chile.—The Red-backed Hawk (*Buteo polyosoma*) is found in South America from Colombia to Tierra del Fuego, along both sides of the Andes, in the Juan Fernández Archipelago off the coast of Chile, and in the Falkland Islands off the Argentine coast (Vaurie 1962, Johnson 1965, Jaksić and Jiménez 1986). The species has been studied little except for its diet and food-niche relationships (Schlatter et al. 1980, Jaksić et al. 1981). Here we report on the behavioral ecology of the Red-backed Hawk, based on a one-year study in central Chile, and draw comparisons with a similar and simultaneous study of the Grey Eagle-Buzzard (*Geranoaetus melanoleucus*) by Jiménez and Jaksić (1989).

Methods.—The study site is described in Jiménez and Jaksić (1989). San Carlos de Apoquindo (33°23′S, 70°31′W, referred to as Los Dominicos in Paynter (1988) is a rugged area 20 km east of Santiago in the Andean foothills, with elevations ranging from 1050 to 1915 m. The physiography includes both flat areas and numerous ridges dissected by deep ravines. The climate is Mediterranean, with cool and rainy winters and dry and hot summers. The wind blows westwardly from the valley to the mountains during the daytime. The predominant vegetation is evergreen scrub that changes physiognomically depending on topography and orientation.

For each Red-backed Hawk we recorded: (1) time and duration of observation, (2) activity type, and (3) habitat beneath the bird. We recognized the following activity types (see Jiménez and Jaksić 1989): (1) thermal soaring, (2) wind soaring, (3) cruising, (4) hovering, (5) harassing, (6) perching, and (7) miscellaneous behavior. We recognized the following habitat types (Jiménez and Jaksić 1989): flatlands, ravines, ridgetops, and slopes (east-, west-, south-, and north-facing). We mapped these habitats and calculated their surface areas (slope-corrected) with a digital planimeter from a high-resolution aerial photograph. The vegetative cover of each habitat type, as represented by trees, shrubs, herbs, bare ground, and rocks was documented by Jiménez and Jaksić (1989), who also estimated prey numbers in these different habitats.

Observations were made from sunrise to sunset, with the day arbitrarily divided into six equal intervals. We made observations every other week between 1 August 1984 and 1 August 1985. We divided a total of 1730 min of observations into four seasons: spring (1

TABLE 1

ABSOLUTE (MIN) AND RELATIVE (%) TIME SPENT BY RED-BACKED HAWKS IN DIFFERENT ACTIVITIES IN CENTRAL CHILE

Activity	Spring[a]	Summer	Fall	Winter
Thermal soaring	22.7 ± 16.5 (14)[b]	21.1 ± 7.0 (12)	11.3 ± 7.3 (6)	2.6 ± 3.4 (4)
% time	48.3	31.2	30.6	27.4
Wind soaring	8.7 ± 8.5 (14)	24.4 ± 12.4 (12)	6.1 ± 3.9 (6)	0.5 ± 1.0 (4)
% time	18.5	36.0	16.5	5.3
Perching	12.7 ± 8.6 (14)	14.3 ± 11.5 (12)	16.2 ± 10.2 (6)	5.6 ± 6.5 (4)
% time	27.0	21.1	43.9	58.8
Cruising	1.0 ± 0.6 (14)	1.8 ± 1.1 (12)	0.4 ± 0.7 (6)	0.7 ± 1.5 (4)
% time	2.1	2.7	1.1	7.4
Hovering	1.3 ± 0.8 (14)	4.3 ± 3.2 (12)	2.4 ± 3.5 (6)	0.0 ± 0.0 (4)
% time	2.8	6.4	6.5	0.0
Harassing	0.4 ± 0.5 (14)	1.0 ± 0.7 (12)	0.2 ± 0.2 (6)	0.1 ± 0.1 (4)
% time	0.9	1.5	0.5	1.1
Other	0.2 ± 0.2 (14)	0.8 ± 0.5 (12)	0.3 ± 0.4 (6)	0.0 ± 0.0 (4)
% time	0.4	1.1	0.9	0.0
Total time	47.0 ± 28.8 (14)	67.7 ± 23.1 (12)	36.9 ± 16.7 (6)	9.5 ± 10.7 (4)

[a] See Methods section for periods involved.
[b] Mean number of min this activity was observed per day ± two standard errors (number of days observed).

August–30 October), summer (1 November–31 January), fall (1 February–30 April), and winter (1 May–31 July). We used one- or two-way ANOVAs for unequal sample sizes (Sokal and Rohlf 1981:210, 360), with PROC GLM in SAS (1985) and the Student-Newman-Keuls test (SAS 1985:444) for *a-posteriori* contrasts. For analyzing frequency data, we used the *G* statistic (Sokal and Rohlf 1981:695).

Results.—Red-backed Hawks were observed throughout the day with no clear peaks of activity in any interval of the day. Although activity levels (measured in absolute time) did not differ among times of the day ($F = 1.57$, df = 5, $P > 0.17$), they did vary with season ($F = 5.39$, df = 3, $P < 0.002$); there was no significant interaction between these variables ($F = 1.57$, df = 15, $P > 0.08$). Red-backed Hawks were most active in summer, intermediately active in spring and fall, and least active in winter (SNK *a-posteriori* test, $P < 0.05$ in all cases). Thermal soaring was the most common flight mode throughout the year, ranging from a spring high of 48% to a winter low of 27% of the observed time (Table 1). Wind soaring was the second most prevalent flight mode, accounting for a high of 36% in summer to a low of 5% in winter. Red-backed Hawks perched from 59% (winter) to 21% (summer) of the time; the remaining activity categories (Table 1) accounted for less than 12% of the daily activity period.

Activity levels (absolute time) differed both among habitat types ($F = 24.27$, df = 6, $P < 0.0001$) and among seasons ($F = 31.92$, df = 3, $P < 0.0001$); there was a significant interaction between these variables ($F = 2.26$, df = 18, $P < 0.002$). Throughout the year, Red-backed Hawks flew more often over ridgetops (from a high of 76% in spring to a low of 3% in winter), north-facing slopes (from 46% in winter to 17% in spring), and west-facing

TABLE 2

ABSOLUTE (MIN) AND RELATIVE (%) TIME SPENT BY RED-BACKED HAWKS ON SEVEN HABITAT TYPES IN CENTRAL CHILE

Habitat type	Spring[a]	Summer	Fall	Winter
Flatland	0.1 ± 0.1 (14)[b]	0.2 ± 0.2 (12)	0.1 ± 0.1 (6)	0.0 ± 0.0 (4)
% time	0.2	0.3	0.3	0.0
Ravine	0.7 ± 0.8 (14)	7.7 ± 5.4 (12)	0.2 ± 0.3 (6)	0.0 ± 0.0 (4)
% time	1.5	11.4	0.5	0.0
Ridgetop	35.6 ± 27.7 (14)	19.9 ± 8.6 (12)	16.5 ± 10.7 (6)	0.3 ± 0.2 (4)
% time	75.7	29.4	44.7	3.2
North slope	7.9 ± 5.1 (14)	21.6 ± 12.0 (12)	15.3 ± 12.1 (6)	4.4 ± 5.6 (4)
% time	16.8	31.8	41.5	46.3
South slope	0.0 ± 0.0 (14)	4.1 ± 2.6 (12)	1.5 ± 2.6 (6)	0.0 ± 0.0 (4)
% time	0.0	6.1	4.1	0.0
East slope	0.4 ± 0.4 (14)	1.3 ± 1.4 (12)	2.3 ± 2.2 (6)	0.1 ± 0.2 (4)
% time	0.9	1.9	6.2	1.1
West slope	2.3 ± 1.7 (14)	12.9 ± 9.0 (12)	1.0 ± 1.0 (6)	4.7 ± 5.8 (4)
% time	4.9	19.1	2.7	49.4
Total time	47.0 ± 28.8 (14)	67.7 ± 23.2 (12)	36.9 ± 38.9 (6)	9.5 ± 10.7 (4)

[a] See Methods section for periods involved.
[b] Mean number of min this activity was observed per day ± two standard errors (number of days observed).

slopes (from 49% in winter to 3% in fall) than over other habitats (Table 2). Except for ridgetops and north-facing slopes, there were seasonal shifts in the use of the remaining habitat types (SNK *a-posteriori* test, $P < 0.05$ in all cases). West-facing slopes, for example, were used more during winter than in other seasons (Table 2).

If Red-backed Hawks used habitat types in proportion to their relative representation in the study area, activity levels should follow the sequence: north-facing slope > south-facing slope > ridgetop > west-facing slope > flatland > ravine > east-facing slope (Jiménez and Jaksić 1989). Instead (Table 2), activity levels in north-facing slopes and ridgetops were significantly higher than those on west-facing slopes and ravines, which in turn were used more than east-and south-facing slopes; activity in flatlands was significantly lower than in all other habitat types (SNK *a-posteriori* test, $P < 0.05$ in all cases). North-facing slopes and ridgetops received more direct solar radiation, and probably generated more thermal drafts, while west-facing slopes received radiation from the setting sun and were swept by the prevailing westerly wind (Jiménez and Jaksić 1989). In contrast, Red-backed Hawks flew infrequently over south-facing slopes (from 6% in summer to 0% in both winter and spring), which were the second most common type of slope in area; they received relatively low amounts of incident radiation and were sheltered from prevailing winds.

The amount of perching in different habitats was not related to their relative availability ($G = 53.1$, df = 5, $P < 0.001$). In 43% of 53 sightings, hawks were perched in north-facing slopes, 36% were perched in ridgetops, 13% in west-facing slopes, and 8% in south-facing slopes. Red-backed Hawks were never seen perching in flatlands, ravines, or east-facing slopes. Thus, habitat types most often used for perching were the same as those used for soaring. Perhaps Red-backed Hawks prefer these perching sites because they afford easy

access to updrafts. Perch substrates were not used homogeneously ($G = 64.4$, df = 8, $P < 0.001$). In decreasing order, perch substrates used were live trees (*Quillaja saponaria,* 32%), standing dead bromeliads (25%), standing dead trees (21%), boulders (13%), and live trees (*Kageneckia oblonga,* 6%), and (*Porlieria chilensis,* 3%). All these structures were above the general level of the scrub canopy and likely provided good visibility and easy access to updrafts for hawks.

Aggressive encounters (harassment), which occurred at a consistent level throughout the year, comprised less than 2% of the Red-backed Hawks' time (Table 1). Red-backed Hawks originated 53 attacks, Grey Eagle-Buzzards 49 attacks (Jiménez and Jaksić 1989). Red-backed Hawks, however, were the second most common victims (48 attacks), after Grey Eagle-Buzzards (recipient of 62 attacks). The relative importance of intra- and interspecific harassment may be assessed by computing the percentage of conspecific, or conversely, allospecific attacks received (Jiménez and Jaksić 1989). Red-backed Hawks were more frequently harassed by other species than by conspecifics (55% allospecific attacks), unlike Grey Eagle-Buzzards (49%), which were about as frequently harassed by conspecifics as by other species. None of these agonistic encounters involved prey, unlike the situation reported by Bildstein (1987) for Red-tailed Hawks (*Buteo jamaicensis*) and Rough-legged Hawks (*B. lagopus*) in south-central Ohio.

Discussion.—Red-backed Hawks did not show any clear daily peaks in activity, but did show clear seasonal pulses (highest activity during summer, lowest during winter). These findings are unlike those reported for Grey Eagle-Buzzards, which showed a clear bimodal pattern of daily activity without seasonal changes (Jiménez and Jaksić 1989). We have no explanation for these species differences. In most other features studied, Red-backed Hawks behaved almost identically to Grey Eagle-Buzzards: (1) their most frequent flight modes were thermal and wind soaring, (2) they flew most often over ridgetops, north- and west-facing slopes, habitats that offered the best atmospheric conditions for soaring, (3) they perched primarily in ridgetops, north- and west-facing slopes, (4) they most frequently perched on live trees of *Q. saponaria,* dead bromeliads, dead trees, and boulders, and (5) they were by far the most aggressive among eight local raptor species (Jiménez and Jaksić 1989).

The similarities in flight activity over the same topographic features may be explained by the favorable updraft conditions afforded by ridgetops, north- and west-facing slopes (Jiménez and Jaksić 1989). As shown by Preston (1981) for Red-tailed Hawks in Arkansas, raptors readily respond to reduced relative humidity and cloud cover, and to increased wind velocity and solar illumination, with more extended soaring. Consequently, we invoke microclimatic conditions as the main determinant of habitat use by Red-backed Hawks (see also Barnard 1986, 1987). But at least two other explanations exist: differences in prey abundance or in prey vulnerability (Wakeley 1978, Bildstein 1987). These alternative hypotheses were evaluated by Jiménez and Jaksić (1989) with regard to Grey Eagle-Buzzards in a study conducted simultaneously at the same site.

Because the pattern of habitat use by Red-backed Hawks is essentially the same as that of Grey Eagle-Buzzards, conclusions drawn for the latter species should hold for the former, given that their diets are very similar (Schlatter et al. 1980). Jiménez and Jaksić (1989) showed that north- and west-facing slopes and ridgetops, where the two raptor species demonstrated the highest activity, had the lowest prey densities (accounting for about 5, 10, and 4% of the mammals captured, respectively). Prey were most dense in ravines, flatlands, east- and south-facing slopes (accounting for about 22, 21, 19, and 19%, respectively, of the mammals captured), but Red-backed Hawks infrequently flew over these habitats.

The other explanation is that Red-backed Hawks hunted on areas with sparse vegetative cover, where prey were more vulnerable, rather than on areas with high prey abundance

(e.g., Wakeley 1978, Baker and Brooks 1981, Bechard 1982, Bildstein 1987). Jiménez and Jaksić (1989) showed that the habitats with the most sparse vegetation were north-facing slopes (most sparse), ridgetops, east-facing slopes, flatlands, west- and south-facing slopes (least sparse). As noted above, east-facing slopes and flatlands were seldom used by Red-backed Hawks, whereas west-facing slopes were frequently visited by them, unlike south-facing slopes. These data indicate that relative habitat use by Red-backed Hawks is not linked closely with relative amounts of sparse vegetation in different habitat types.

It appears that Red-backed Hawks key on habitat types due to updrafts rather than prey density or vulnerability as reflected in the degree of vegetational sparseness. This conclusion concurs with that of Barnard (1986, 1987) for three South African raptors, and of Jiménez and Jaksić (1989) for Grey Eagle-Buzzards at the same site in central Chile. However, this conclusion does not appear to hold for North American buteos (Wakeley 1978, Baker and Brooks 1981, Bechard 1982), probably because the North American studies were done in flat or rolling terrain with a relative scarcity of updrafts.

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Poult adoption in Merriam's Wild Turkeys.—There are few documented cases of gallinaceous birds caring for offspring other than their own. Willow Ptarmigan (*Lagopus lagopus*) usually mate monogamously, with pairs remaining together throughout the breeding season, but they occasionally are polygynous (Hannon 1984, Martin and Cooke 1987, Martin 1989). If males are removed from monogamous pairs after breeding, replacement males may fill the openings and adopt the brood (Martin 1989). We observed four cases of apparent adoption by Merriam's Wild Turkeys (*Meleagris gallopavo merriami*) during 1987, 1988, and 1989 while collecting data to determine dispersion and habitat selection patterns in a ponderosa pine (*Pinus ponderosa*) ecosystem in the central Black Hills of South Dakota. Adoption by Merriam's Wild Turkeys, to our knowledge, has not been documented previously. Merriam's Wild Turkeys are polygynous, and the young are cared for and reared by hens.

On July 25, 1987, a radio-fitted hen was observed with five poults. In the week that followed, she was located twice with another radio-collared hen, which had four poults. On August 3, 1987, the first hen was observed brooding alone with two poults, and the second hen was observed with seven poults. The second hen appeared to have adopted, at least temporarily, three poults from the first hen. The nearest possible relationship between these two hens was estimated to be half-siblings.

On June 13, 1988, four days post-hatch, a hen with a radio transmitter was flushed from a ground roost. No other hens were in the vicinity. The poults scattered throughout the vegetation except for one which flew approximately 30 m into a ponderosa pine tree. Some turkey poults are capable of flying 1–2 m when they are 8 days old and are strong flyers by 18 days (Bailey and Rinell 1968, Williams 1974). Based on the size of this poult and its flight capability, we believe this poult was obtained from another brood.

On June 27, 1988, a different radio-collared hen was observed brooding two poults 19 days after certain complete loss of her brood. These apparently adopted poults had an estimated age of two weeks, and we observed this hen three times (once on roost) with these poults when no other hens or poults were in the immediate vicinity. The hen was observed alone a week later and we do not know the fate of the poults.

The fourth observation occurred on June 5, 1989. A radio-equipped hen was observed brooding two poults one day after only two of eight eggs in her clutch had hatched. Nine days later, this hen was observed with four poults; no other hens were in the vicinity. The hen appeared to have adopted two poults. The hen was observed with three to four poults on several occasions during the next four weeks. One poult remained until joining two other hens and their poults.

Plausible explanations for adoption by turkeys may include the following. Prolonged close association between the parents and offspring bring the young into intimate contact with subsequent broods of the parent birds (Skutch 1961). The adopter may benefit by gaining

experience in parenting activities which could enhance reproductive success later in life, but the costs would be lost initial reproductive success (Selander 1964, Brown 1978). When helpers are related and when the benefit/cost ratio is large, we might expect selection to lead to greater social specialization (Brown 1978) such as adoption. However, in our observations, the adopters were mature hens; thus, there would be little reproductive experience gained since two of the four hens were successful in previous years, and three had existing broods. In contrast to the other situations, costs to the hen on the June 27, 1988 observation were low. This hen had lost here complete brood, and we had not observed renesting following hatching of a brood. The benefit/cost ratio in this situation would have been larger. Since in the Black Hills the risks of dispersing from the family units are minimal, mates and territories are plentiful, and initial breeding success is high, the establishment of family social units and adoption should be rare (Emlen 1982).

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Diurnal foraging by Spotted Owls.—The Spotted Owl (*Strix occidentalis*) is thought to be one of the most nocturnal of North American owls (Bent, Life histories of North American birds of prey, U.S. Natl. Mus. Bull. 170, 1938). However, Miller (Miller, The book of owls, L. W. Walker, ed., Alfred Knopf, 1974) observed them foraging ". . . at all hours of the day or night . . ." while they were feeding young in Marin County, California. Forsman (Forsman et al., Distribution and biology of the Spotted Owl in Oregon, Wildl. Monogr., 1984) observed very little diurnal foraging during their studies of Spotted Owls in Oregon, concluding that

TABLE 1
DATE, TIME (PDT) AND DISTANCE FROM NEST DURING DIURNAL FORAGING BOUTS BY BREEDING SPOTTED OWLS

Individual	Date	Time	Distance (km)
Gaddis female	7 July	1200	1.0
Gaddis male	8 July	1045	1.4
Gaddis male	11 July	1230	1.5
Gaddis male	15 July	1000	0.8
Gaddis female	15 July	1230	1.1
McCulloh male	13 July	1100	0.7
McCulloh male	30 July	1230	1.0
McCulloh male	7 August	1130	1.5
Wallace male	8 August	1300	1.4

the few diurnal foraging bouts observed were opportunistic, and they suggested that Miller's observations of diurnal foraging were most likely also opportunistic.

I collected pellets from four breeding and 13 nonbreeding pairs of Spotted Owls near Georgetown, El Dorado County, California. Prey were identified to species from pellet contents and divided into diurnal and nocturnal categories, based on their life history patterns. I attached radio transmitters to six pairs of Spotted Owls, using a backpack configuration and a teflon-tubing harness. I tracked the owls to their roosting sites using a receiver and two-element Yagi antennae. I define foraging as an active search for prey, as opposed to opportunistic foraging, which I define as taking prey if it presents itself.

During 1982, Spotted Owls captured a relatively high proportion of diurnal prey. Prey items were identified from seven pairs of owls (N = 572 prey items); 10% were diurnal birds and 4% were diurnal mammals. I noted that 20% of the 208 prey items from the breeding pair were diurnal, while 10% of the 364 prey items taken by the six nonbreeding pairs were diurnal. This was a statistically significant difference ($\chi^2 = 11.34$, df = 1, $P < 0.001$).

During 1983, I placed radio transmitters on four pairs of Spotted Owls. One, the Gaddis pair, was breeding, and the other three were not. I tracked each of these eight owls to diurnal roosts on ten occasions, approximately one week apart, during the summer. On 7 July, after the young had fledged but were still dependent, I tracked the Gaddis female to a daytime roost 1 km NW of the nest site. The female was roosting in the sunlight in a Douglas fir (*Pseudotsuga menziesii*) (Table 1). Canopy closure around the roost site was much lower than most summer roost sites. The bird was obviously foraging rather than roosting. She was alert, reacting to every sound and staring intently at a nearby incense cedar (*Libocedrus decurrens*). As I watched, she suddenly left her perch, gliding towards the cedar, plucked a long-eared chipmunk (*Eutamias quadrimaculatus*) from the trunk near a stick nest 9 m above the ground and immediately returned to the Douglas fir with her prey. She lost her grip on the chipmunk, which fell to the ground and immediately ran to the safety of a brush pile. I found the Gaddis female foraging diurnally on one other occasion and found her mate foraging diurnally on three occasions (Table 1). On 17 July, both of the Gaddis juvenals were killed by a predator. The next day, both the male and female stopped foraging diurnally and became predominantly nocturnal.

During 1984, two breeding pairs were equipped with radio transmitters. I tracked each of these four owls to diurnal roosts on ten occasions, approximately one week apart, during

the summer. The male of the McCulloh pair was observed foraging diurnally on three occasions (Table 1). During a foraging bout on 7 August he caught a Douglas squirrel (*Tamiasciurus douglasii*). The Wallace male was observed foraging diurnally once on 8 August.

All nine diurnally foraging owls were found between 1000 and 1300 PDT (Table 1). In all nine cases of the 50 visits to roosting Spotted Owls with young, the owls were alert to motion and sound and were not drowsy as I normally found them when roosting in the daytime. In addition, in all cases, the owls were at a greater distance from the nest site than normal. The mean distance was 1.2 km and the range was 0.7 to 1.5 km (Table 1). I generally found roosting owls with young within 0.1 km of the nest. During seven of these nine cases, they were at sites where they would not normally roost in the summer due to scant canopy closure. The canopy closure at these nine sites ($\bar{x}$ = 63.6% ± 10.5 [2 SE]) was significantly lower ($P < 0.01$) than at 120 summer roosting sites ($\bar{x}$ = 85.8 ± 3.9 [2 SE]) (Laymon, The ecology of the Spotted Owl in the central Sierra Nevada, California, Ph.D. diss., Univ. of California, Berkeley, 1988).

Nonbreeding Spotted Owls that I visited 70 times during 1983 and 1984 were not observed foraging during daylight hours even though 14% of their 627 prey items were diurnal. It is likely that some of these food items were captured opportunistically and that others were captured at dawn and dusk. The breeding birds, however, based on a sample of 445 prey items captured 25% diurnal prey. This difference was statistically significant (χ^2 = 21.79, df = 1, P = 0.0001). When the proportion of foraging bouts vs visits is compared for breeding (18% of 50 visits) and nonbreeding owls (0% of 70 visits) the difference is also significant (χ^2 = 12.07, df = 1, $P < 0.001$).

Forsman and colleagues believed, based on their data from Oregon, that Spotted Owls did not forage diurnally and captured diurnal prey opportunistically. Unlike Forsman et al. (1984) and in agreement with Miller (1974), I found that Spotted Owls in the Sierra Nevada captured more diurnal prey and regularly foraged diurnally to feed their young during the first six weeks following fledging. The observations of diurnal foraging presented here must represent a small proportion of the actual diurnal foraging of these breeding birds, since each owl was tracked to a daytime roost only 10 times during the summer and was observed for an hour each time. On six occasions, out of approximately 20 visits, adult owls were seem bringing food to their young during the middle of the day.

The immediate change exhibited in foraging behavior when the young of the Gaddis pair were killed suggests that the need to provide food for the young was the stimulus that led to their diurnal foraging. It is likely that diurnal foraging is a reaction to food stress placed on the adult Spotted Owl by rearing young. It is also possible that only pairs that commit to intensive diurnal foraging are able to raise young in the disturbed environment where this study was done. Spotted Owls in less disturbed areas, with more abundant preferred nocturnal prey, might not forage diurnally during the breeding season.

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Winter recoveries and territorial affinity of Common Loons banded in Wisconsin.—Although the wintering range of Common Loons (*Gavia immer*) is well known (Bent 1919, Palmer 1962), little information is available relating individuals marked during the breeding season to their specific wintering areas. McIntyre (1988) suggested that Minnesota loons winter along the Gulf Coast of Florida and that loons wintering along the Atlantic Ocean breed in mid-Canada. Eberhardt (1984) reported one adult and three juvenile winter recoveries from Florida. Additionally, little information is available regarding territorial affinity. McIntyre (1974) recaptured a loon that was banded on the same lake the year before. Eberhardt (1984) recaptured six of 28 adults and one of 128 juveniles on the same lake where they were banded the year before. We present recovery information that supports territorial affinity and documents wintering areas of Common Loons from Wisconsin.

Loons were captured using night-lights (Bishop and Barrat 1969), modified commercial pound-nets, and a spring-driven bow net that incorporated a decoy and broadcasted tremolo and yodel calls. We marked 20 adults and 34 chicks with standard U.S. Fish and Wildlife Service leg or toe bands (McIntyre 1977), thirty-five of which also received patagial tags and/or colored leg bands (Strong et al. 1987a).

We recorded five (three adult and two young) winter recoveries. The three adults (probably non-breeders) had been marked during June 1987 on Lake Superior along the Apostle Islands National Lakeshore, Bayfield Co., Wisconsin. Two were found dead: one was recovered near St. Petersburg, Florida, during December 1987, and the other near Pensacola Beach, Florida during July, 1988. The third adult was entangled in a fishing net during spring 1988 on Lake Arrowhead, near Atlanta, Georgia and released unharmed.

The two young loons were banded from two different broods during June 1986 on the Turtle-Flambeau Flowage (TFF), Iron Co., Wisconsin. One loon was observed during March 1988 on Lake Walter F. George, near Eufaula, Alabama (J. W. McIntyre, pers. comm.), while the other was found dead during May 1988 on Santa Rosa Island, near Pensacola, Florida.

We also recorded four summer recoveries. Three loons were marked during July 1987 on the TFF and were members of nesting pairs. All three loons were observed periodically during summer 1988, and one was also observed during summer 1989. We found them in, or adjacent to, the same territories that they had occupied during 1987. We do not know whether these loons nested during 1988 or 1989. One adult loon, originally captured as a member of a breeding pair on Mirror Lake, Iron Co., Wisconsin was observed once on the same lake during May 1986. However, we found no evidence of nesting on Mirror Lake during 1986.

These observations, along with information summarized by McIntyre (1988), suggest that Common Loons from the western Great Lakes area winter along the Gulf Coast. However, the migration route remains unclear. Common Loons from this area may migrate along the Great Lakes and St. Lawrence River to the Atlantic Ocean, then fly south along the coast to their wintering areas. McIntyre (1988) reported several recoveries that support this possibility. Another potential migration route is a north/south route to the Gulf of Mexico. Boyle et al. (1979) suggested that Common Loons migrated overland. Powers and Cherry (1983) noted that Common Loons used both inland and offshore routes. Common Loons have been reported in Oklahoma, Kansas, and Texas, however, no banded birds have been recovered along this route (McIntyre 1988).

Territorial affinity is more likely to occur in long-lived species. Common Loons are probably long-lived with low adult mortality rates (Nilsson 1977, McIntyre 1988). Strong

et al. (1987b) found high reuse of territories and nest sites. Territory reuse would be advantageous, requiring less time spent searching for suitable habitat in an environment with a short ice-free season (Yonge 1981).

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Nesting of the Common Diuca Finch in the central Chilean scrub.—The Common Diuca Finch (*Diuca diuca*) is abundant in central Chile (Cody 1970), but its nesting behavior is poorly known. Goodall et al. (1946) reported that Diuca Finches build an open nest made of grass and roots and place their nest in various species of shrubs and trees. However, occasional observations indicate that Diuca Finches exhibit more varied nesting behavior. In some cases the nest is camouflaged and in others the nest is conspicuous. In this paper, we examine the selection of nest site and nest lining by Diuca Finches in the scrub zone of central Chile and discuss the possible role of predation.

Methods.—The study area was located in San Carlos de Apoquindo, 20 km E of Santiago (33°24'S, 70°30'W). This locality was vegetated by a scrub formation named matorral, with dominant associations of evergreen shrubs such as quillay (*Quillaja saponaria*) and litre (*Lithrea caustica*), both with an average height of 6 m. Summer deciduous shrubs were represented by trevo (*Trevoa trinervis*), crucero (*Colletia spinossisima*), espino (*Acacia caven*), and colliguay (*Colliguaja odorifera*) (average height was 3 m). The climate was of Mediterranean type, with winter rains and summer drought (di Castri and Hajek 1976).

The nests of Diuca Finches were located by observing the behavior of adult birds during the reproductive period (October 1987 to February 1988) and by examining all plants in a 3.1 ha area. We determined plant species, presence or absence of thorns, foliage density, height of nest, nest lining material (smooth or thorny twigs, average diameter 1.5 mm), and presence of eggs and chicks. We computed a periphery index as the ratio of trunk-to-nest distance divided by the canopy radius at nest height. Shrubs used by finches for nest sites were either thorny and low leaf density (Crucero, Trevo, and Espino) or thornless and high leaf density (Quillay).

We estimated the canopy-projected cover of shrubs and trees with the line intercept method (Armesto and Gutierrez 1980), along a 500-m transect.

We checked whether the selection of nest sites was random by comparing expected with observed frequencies by means of a χ^2 test (Sokal and Rohlf 1981). The expected number of nests was calculated by applying the proportion of plant cover in which Diuca Finches nested. To determine whether dependence existed between selection of nesting material and nesting sites, we analyzed the relative frequencies of nests built with smooth or thorny material by means of χ^2 test (Sokal and Rohlf 1981) for nests located in thornless and high leaf density plant structure. The expected number of nest types was calculated by applying the proportion of plant cover of all plants that could supply smooth or thorny material. When the expected number of nests with thorny or smooth nest lining material was less than five, Fisher's exact test (Sokal and Rohlf 1981) was used.

Eleven nestling Diuca Finches (occupying five different nests) were watched from the egg stage until fledgling stage every five days, in order to estimate their mortality up to the moment of nest abandonment. Nesting parents did not appear unduly disturbed by our observations and none deserted the nest.

Results.—4.05% of the shrubs examined were used for nesting by Diuca Finches (Table 1). Diuca Finches nested on four of the nine shrub species present, which together represented 57.8% of the plant cover available (Table 1).

Diuca Finches appeared to prefer building their nests in canopies with both high leaf density and no thorns ($\chi^2 = 11.39$, df = 1, $P < 0.005$), especially in quillay (Table 1). In this case, there was no apparent selection of nest lining material ($\chi^2 = 0.007$, df = 1, $P < 0.9$).

TABLE 1

PLANT CHARACTERISTICS IN THE STUDY (3.1 HA), NUMBER OF DIUCA FINCH NESTS, AND TYPES OF NEST LINING ON EACH PLANT SPECIES

Plant species	Number of shrubs	Relative cover (%)	Number of *Diuca* nests	Nest lining	
				Thorny	Smooth
Quillaja saponaria[a]	93	18.8	16	6	10
Colletia spinossisima[b]	39	14.2	4	4	0
Trevoa trinervis[b]	123	23.4	3	2	1
Acacia caven[b]	10	1.4	2	2	0
Lithrea caustica[a]	82	13.1	0		
Colliguaja odorifera[a]	88	12.4	0		
Baccharis linearis[a]	177	15.5	0		
Azara dentata[a]	4	1.2	0		
Talguenea quinquinervia[b]	2	0.2	0		
Total	618	100	25	14	11

[a] Thornless and high leaf density.
[b] Thorny and low leaf density.

Diuca Finches chose thorny nest lining material (Fisher's exact test, $P < 0.001$) when they nested in shrubs with thorns and low leaf density. However, they seemed to avoid nesting in these types of shrubs in spite of the large availability of this plant type (39% of total relative cover). In the latter case, birds chose thorny material (Table 1) for lining their nests. The periphery index indicates that there were no significant differences in location of nests between the two types of plant structures recognized (Student's *t*-test, not significant), one with thorns and low leaf density (average PI = 0.44, SD = 0.11) and the other thornless and high leaf density (average PI = 0.66, SD = 0.066).

Observations of birds from egg through fledgling stage indicated that mortality before leaving the nest was 82% (Fig. 1). During the study period, we noted picked eggs, missing eggs, and chicks. Feathers of a raptor, the Chimango Caracara (*Milvago chimango*), were found inside one Diuca Finch nest where two eggs had disappeared.

Discussion.—Nilsson (1986), Moller (1987), and Martin and Roper (1988) have indicated that nest-site characteristics and nest-building material are determined mostly by differential predation on nests which differ in such characteristics. Birds appear to have the capability of responding behaviorally to reduce predation effects (Nilsson 1986, Jaksić and Simonetti 1987, Graham 1988). Our results indicate that Diuca Finches are subject to high mortality before leaving the nest. According to Ricklefs (1969), predation is the most important factor of mortality in eggs and chicks among several orders of birds, including Passeriformes.

Predation may be a factor in the high mortality observed in Diuca Finches. Jiménez and Jaksić (1989) showed that the Austral Pygmy-Owl (*Glaucidium nanum*) is an important predator of Diuca Finches (eggs and nestlings). Núñez (pers. comm.) has seen mouse-opossums (*Marmosa elegans*), racerunners (*Callopistes palluma*), and snakes (*Philodryas chamissonis*) eating eggs and chicks of Diuca Finches.

The nesting pattern observed among Diuca Finches could thus be related to avoidance of predation through selection of plant structures with high leaf density that provide crypsis against predators to the nests (Nilsson 1986). Or alternatively, in the case of conspicuous nests built in plants with thorns and low leaf density, the selection of thorny material for the nest lining could be favored and would counteract predators' efficiency. The alternative

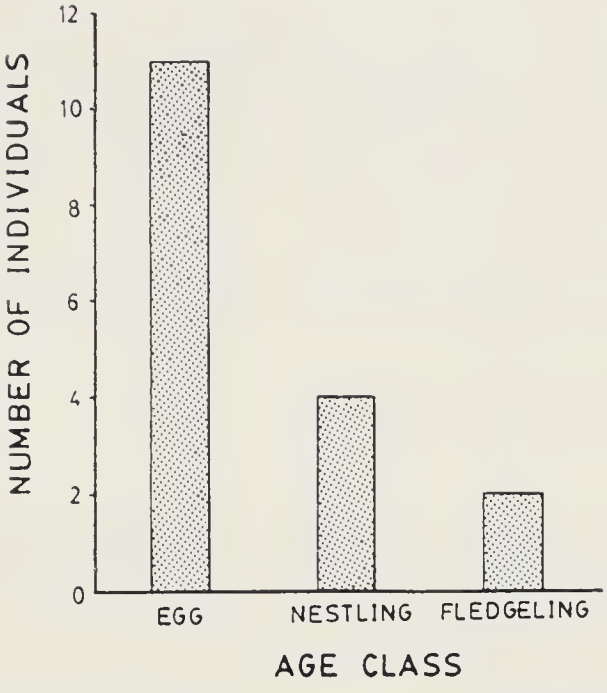

FIG. 1. Survival of *Diuca* Finch eggs, nestlings and fledglings in the nest.

hypothesis that nest lining material is collected near the nest cannot explain the random selection of nest lining material in both thornless and high leaf density plant structure. In addition, the authors observed Diuca Finches collecting nest lining material in an area 50 m around the nests.

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The proximate costs and benefits of polygyny to male Northern Shrikes.—Trivers (1972) defined parental investment as any investment by a parent in an offspring that increases the offspring's chance of surviving at the cost of committing resources to other offspring. Wittenberger (1981) modified this definition to apply to entire clutches or broods of offspring. An exact definition of parental investment has been disputed for some time, and even today the debate continues. Discussions of mating strategies typically deal with the benefits and cost of a behavior to females (e.g., Orians 1969, Alatalo et al. 1986). The consequences for males, however, are less often addressed. For example, polygyny has obvious benefits over monogamy for males because a polygynous male has a greater reproductive potential during a single breeding season. However, polygyny may also impose higher costs to the male if he contributes to the care of offspring. If there is a cost of polygyny to the male it is ultimately paid for in reduced survivorship, which unfortunately is difficult to measure because it requires large sample sizes and long-term studies. But, even proximate measures of cost, such as the time involved in feeding and defending additional young, may be informative because time spent in parental care probably exposes the male to additional hazards of predation and injury (Reid and Sealy 1986). Proximate costs to males might also be relevant to mate selection. In fact, some theories of mate selection assume that females choose among males on the basis of the male's ability to incur proximate costs (Slagsvold 1986, Alatalo et al. 1986).

We investigated some of the proximate costs of polygyny to male Northern Shrikes (*Lanius excubitor*). In Israel, male Northern Shrikes reside permanently in breeding territories. Females are not permanent residents and leave the breeding area immediately after their broods fledge. Seven male Northern Shrikes were observed during the 1987 breeding season, from January to June, at Sede Boqer (34°47′N, 30°52′E, 475 m ASL), in the Negev Desert highlands of Israel. The study area is a flat loessal plain. The plateau supports a sparse dwarf shrub community dominated by *Hammada scoparia, Zygophyllum dumosum, Reaumuria hirtella, Anabasis syriacus,* and *Artemesia herba-alba.* The major woody species are *Tamarix nilotica, Atriplex halimus, Retama raetam,* and *Thymelaea hirsuta.* Regional flora includes a large variety of herbs and geophytes (Danin et al. 1975).

Two of the seven males we observed had polygynous relationships (Yosef and Pinshow 1988b); the first two documented cases of polygyny in this species. Following this discovery, time-budgets were constructed for all seven pairs under observation. The birds' diurnal behavior was divided into the following categories: (1) perching, (2) flying (usually to or from collecting prey, or chasing conspecifics or heterospecifics from the area, or changing lookout points), (3) handling prey (recorded from the instant the shrike landed on or near the prey and attacked it until the prey was impaled or consumed), and (4) preening.

TABLE 1
AVERAGED TIME-BUDGETS AND DIETS OF POLYGYNOUS AND MONOGAMOUS MALE NORTHERN SHRIKES

	Polygynous males (N = 2)	Monogamous males (N = 5)
Time budgets		
Total hours of observation	216.0	186.0
Percent total:		
Perched	82%	69%
Flight	2%	2%
Handling prey	2%	1%
Preening	12%	32%
No. of occasions seen feeding nestlings	0	17
Diets		
Number of prey taken	256	109
Percent total:		
Arthropods	89%	95%
Reptiles	7%	4%
Birds	3%	—
Mammals	0.4%	—
Vertebrates : arthropods ratio	0.12:1	0.04:1

We observed the two polygynous males for a total of 216 h and the five monogamous ones for 186 h on 56 days. All seven males were captured with a bal-chatri noose trap, color-banded and released. Territories were mapped by plotting points of shrike activity and by observing the reaction of the males to taped songs of other males and to a mounted specimen. Birds were sexed by observing mating and other behavior. As far as was possible, all prey taken were identified by observing the birds with the help of binoculars or a telescope, or by inspecting impaling sites. The birds and their mates were observed through a complete breeding season, and clutch size, hatching success, and number of nesting attempts were recorded. Because the exact number of young that fledged from each nest could not be determined, we indexed the seasonal fitness of each male by the total number of eggs laid in nests in his territory. During this stage of the research, it was still unclear why some of the young disappeared from their nests at the very early stage of approximately 10 days of age. It was later determined that parents often transferred their young to the base of neighboring trees or bushes (Yosef and Pinshow 1988a).

We compared polygynous and monogamous males with respect to the time spent in prey detection and handling. Territory quality was the uncontrolled variable. Comparisons between contemporaneous observation periods of fixed length revealed that polygynous males spent significantly more time than monogamous males seeking prey ($Z = 3.74$, $P < 0.0003$, $N = 56$) and handling prey ($Z = 3.92$, $P < 0.0001$, $N = 43$) (Wilcoxon's signed rank test, Steele and Torrie 1980). Males usually brought food to the vicinity of the nest and passed it on to the female or impaled it at cache sites. Females were seen to retrieve such food by themselves. Polygynous males were never seen feeding or attending their young directly, although monogamous males were observed to do so on 17 occasions (Table 1).

Monogamous males caught 0.59 prey per hour (109/186 h), compared to 1.19 prey per

TABLE 2

SIZES OF TERRITORIES, NUMBER OF NESTS AND NUMBER OF EGGS LAID BY MATES OF MALE NORTHERN SHRIKES

	Territories defended (ha)	Number of nestlings	Number of eggs laid
Polygynous males			
#1	76.9	3	16
#2	72.7	4	21
Monogamous males			
#1	54.8	2	11
#2	68.8	1	12
#3	59.2	2	10
#4	55.3	2	10
#5	56.9	2	11

hour (256/216 h) for the polygynous males. The diet of monogamous males consisted mainly of arthropods (95.4%), the rest being lizards (4.6%). Although polygynous males also took mainly arthropods (89.4%), they also hunted a variety of vertebrates including reptiles (7.4%), passerine birds (2.7%) and small rodents (0.4%). A comparison of the arthropod vertebrate ratio shows that polygynous males handled three times as many vertebrates as did monogamous males (0.12:1 vs. 0.04:1).

Polygynous males defended significantly larger territories than did monogamous males (Mann Whitney Test $U_{(0)2,5} = 10$, $P < 0.05$) (Table 2). There was also a significant difference in the total number of nesting attempts during the season for each male: 3.5 ± 0.7 attempts for the polygynous males and 1.8 ± 0.5 for monogamous males ($U_{2,5} = 10$, $P < 0.05$) and the mates of polygynous males laid significantly more eggs (18.5 ± 3.5 vs 9.4 ± 2.5) ($U_{2,5} = 10$, $P < 0.05$).

If all the eggs laid by each female resulted from within-pair copulations, then polygynous males produced nearly twice as many eggs as did monogamous males. However, increased egg production was not without cost: polygynous males hunted more intensively on exposed sites and may have been exposed to greater predatory risks and energetic costs. The significant difference in time, and probably energy, spent by polygynous males in seeking and handling prey seemed to be at the expense of their personal upkeep, i.e., they spent less time preening or in other maintenance upkeep behavior (Table 1).

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ORNITHOLOGICAL LITERATURE

WHERE HAVE ALL THE BIRDS GONE? By John Terborgh. Princeton Univ. Press, Princeton, N.J. 1989: xvi + 207 pp., 35 black and white photos, 18 graphs and maps. $40 (hardcover), $14.95 (paper).—As I write this review, the northbound warbler migration is in full swing. Full swing? Well, it is merely a shadow of the great flights I remember from 40 years ago. Or is it? Does memory play tricks on me or are there fewer warblers today? Ornithologists and birders have argued about the status of warblers and other Neotropical migrants for some time. If these species are indeed declining, is it because of changes occurring in the breeding range or in the wintering range? Do the migrants use the primary tropical forest or are they mostly in the second-growth? These are some of the contentious points and several symposia have been devoted to these birds and the factors affecting them. Now comes John Terborgh, a knowledgeable and experienced tropical ecologist, with a book subtitled, "Essays on the biology and conservation of birds that migrate to the American tropics."

Terborgh starts with a summary of his boyhood experiences in rural Virginia, not far from Washington, and then discusses the great changes that took place as the area was "developed." From this anecdotal base, he proceeds to present some harder data. He analyzes the observed declines as shown by two long-term breeding bird censuses taken near Washington. Over the years, the populations of these were reduced by 45%, and many species disappeared completely. This has generally been attributed to the fragmentation of the habitat in the region surrounding these study areas. Most of the affected species were the area-sensitive species which do not do well if forced to nest too near to a habitat edge. After a careful consideration of the data, and the results of several experimental studies, Terborgh concludes that the main factors influencing these populations are increased nest predation and increased parasitism by the Brown-headed Cowbird (*Molothrus ater*). Quiz time! Is there any relation between the adoption of the mechanical cornpicker and the population of Hooded Warblers (*Wilsonia citrina*)?

Turning to the question of deforestation in the tropics, Terborgh finds that the few hard data available are not in agreement, although suggestive. Terborgh feels that loss of the tropical forest is not YET an important factor for most birds. He does, however, offer the interesting suggestion that the disappearance of Bachman's Warbler (*Vermivora bachmanii*) may be due to the replacement of most of the Cuban forest by fields of sugar cane.

The heart of the book is the sequence of chapters discussing the migrants and their migrations. In these chapters, he combines his own considerable observations with suitable data from the not altogether adequate published literature to provide some answers to many of the questions that arise. These chapters summarize much of what is known, little as it is, of the migrants in their winter ranges.

Where do the migrants come from? Most of them are from eastern North America, particularly the great eastern deciduous forest. Where do they go? The bulk of them winter in Mexico, the Bahamas, and the Greater Antilles. What habitats do they occupy in the tropics? Contrary to the ideas held earlier, migrants are most common in the primary forests. Relatively few of them go to the lowland forests, and at middle elevations migrants are more common than residents. Unfortunately, it is at middle elevations that the greatest human pressure occurs. Why do the birds migrate in the first place? Terborgh ascribes the urge to migrate almost solely to changing food resources. He does offer a balanced discussion of the old argument as to whether the migratory species originated in the temperate zone or in the tropics.

Terborgh points out that one can make few broad statements and must almost treat each

species individually. Some of the migrants maintain winter territories, some join in flocks, both single species and mixed, some are solitary, and some join the ant-following flocks of resident birds.

In the chapter called "A Glimpse of Some Tropical Habitats" he describes vividly the changes observed when a patch of Ecuadorian cloud forest studied earlier was converted to a cow pasture. This is contrasted with the changes reported for a Yucatan milpas area. While pointing out that the milpas method of farming practiced for centuries has not harmed the avifauna greatly, Terborgh reminds us that this primitive agricultural practice is almost a thing of the past. His worst case scenario describes the almost total destruction of the mangrove forest in Ecuador to promote the shrimp industry. A somewhat more optimistic "best case" is the similarity of coffee plantations, with their tall shade trees, to an imperfect replica of the primary forest. Terborgh does not, however, mention the latest development, the introduction of coffee trees that do not require shade.

While much emphasis has been placed on the removal of tropical forests, little note has been made of the conversion of the South American pampas into monoculture croplands. Several shorebird species winter in this area and are under resulting stress. It is pointed out, however, that the birds that nest in the North American tall-grass prairie are not really affected by current events in South America. Their breeding habitat has already been almost totally eliminated in the United States, and further events in the south can have little effect.

A thoughtful chapter on "The Whys and Wherefores of Deforestation" points out that in the United States we still have some forest left, because we had a treeless area of fertile soil, the great prairies of mid-continent for growing our food. Most European countries lacked this and thus have little forest remaining. The countries of the Neotropics also lack this cushion, and so while the rate of deforestation in the tropics is about the same as the rate at which the North American forest was removed, the results in the south will be much different.

It is obvious that the passerine population in the eastern United States must be less than it was in pre-colonial times, since the present-day forests are only about 60% of the original. But given the poorer quality of much of the present forest and the extent of fragmentation, Terborgh estimates that the population may be only one-quarter of what it was 400 years ago. If this is the case, we may have to wait until three-quarters of the tropical forest is gone before the effects will be noticeable. At that time, it may be too late to do anything about it.

The book closes with a thoughtful chapter on conservation, mostly conservation in the tropics, but also with some pertinent suggestions for U.S. citizens. Terborgh points out that most people in the tropical countries want to live in the cities, but lack of jobs forces them into the countryside with resultant destruction of the forest. Short-sighted governments, indeed, encourage this. In the long run, such a program is doomed to failure. Terborgh suggests that tropical forestry could be a hope for the future and something like the multiple-use management extolled (but often not practiced) by the U.S. Forest Service might work in the tropics.

For North Americans he gives a list of issues for political action and several "matters for individual discretion." One of these is a heretical idea that will raise many eyebrows. Perhaps the indiscriminate feeding of birds in the winter should be given second thoughts. Besides making things nice for chickadees and cardinals, it helps raise the populations of nest predators such as Blue Jays (*Cyanocitta cristata*) and Common Grackles (*Quiscalus quiscalus*), as well as nest parasites like the cowbird.

This is an important book which should be, and no doubt will be, read by all interested in birds or other aspects of the environment. Terborgh, as a scientist, has attempted to present a factual exposition of this subject, and in this aim he has most definitely succeeded.

I recommend the book to all, but I suppose that it is too much to expect that congressmen, cabinet officers, or other policy makers will ever read it.

Since Terborgh wrote this book, a number of things have happened in this fast-changing field. The symposium on Neotropical Migrant Landbirds held in December 1989, in which Terborgh was keynote speaker, presented many more hard data on these birds. The picture was no brighter. Of great significance was a paper by Robbins, Sauer, Greenberg, and Droege (Proc. Natl. Acad. Sci. 86:7658–7662[1989]), which utilized Breeding Bird Survey data to show that many of the migrant species in the eastern forests had undergone precipitous declines in the period 1978–1979, while the short distance migrants and permanent residents had shown little change. Perhaps the critical "break even" time when tropical deforestation begins to be more important than habitat change in the north is already on us. The publishers of *Bulletin of the Atomic Scientists,* in light of current international developments, recently turned back by several minutes their logo, the "Doomsday Clock," which since the 1940s had ticked off the time until the holocaust of nuclear war. If such a clock exists for the migrant birds, perhaps there are not many minutes left until midnight.—GEORGE A. HALL.

ORNITHOLOGY. By Frank B. Gill, illus. by James E. Coe. W. H. Freeman and Co. Publishers, New York, New York. 1990: 672 pp., 363 figs., 35 tables. $49.95.—Congratulations to Frank Gill. His new book, "Ornithology," is a remarkably comprehensive survey of the entire field of the biology of birds. Its intended audience is undergraduate students and their instructors, and it will set a new standard for teaching in the field. Because it contains a significant and well-balanced summary of the science of ornithology, including research findings right through the 1980s, it will be an important addition to any library, personal or public.

The organization of the book makes it easy to use. The six parts are Origins, Form and Function, Behavior and Communication, Behavior and the Environment, Reproduction and Development, and Populations. Each of these parts contains three to five succint chapters plus a few recommendations for further reading. Within this framework, Gill's easy narrative style belies the high level of scholarship required to pull together and evaluate the literature on so many subjects. The bibliography contains more than 1500 citations. In the Preface, the instructor is advised to select among chapters so as to tailor a one-semester course to particular areas of interest.

The book is generously illustrated with over 350 photographs, graphs, and drawings. Tables, mathematical models, and statistical tests are minimized. The first of two appendices is a 62-page survey of the birds of the world by orders. This section is illustrated with more than 100 excellent bird portraits by James E. Coe. Guy Tudor served as consultant for the bird portraiture. This appendix is a modern version of the section in "Fundamentals of Ornithology" (1959, John Wiley and Sons, Inc.) by Gill's academic ancestors at the University of Michigan, Josselyn Van Tyne and Andrew J. Berger. Gill's version follows the taxonomy of the reference list of the birds of the world by Morony and coworkers (1975, American Museum of Natural History) and the sixth edition of the A. O. U. Check-list of North American Birds. English and scientific names of each of the 9021 species of birds are given in Appendix II.

Gill points out areas of ornithology that are of current interest, areas where there is disagreement, and areas where progress awaits new ideas and techniques. He discusses the various kinds of evidence that have been used to support different positions on controversial issues. His conceptual approach throughout is evolutionary.

Gill's enthusiasm for the intellectual challenges of his subject is especially apparent in his discussions of recent research. In section 1 on Origins, he gives examples of how morpho-

logical, paleontological, and molecular data contribute to the analysis of how groups of birds are related to one another. Are flamingos derived from storks, ducks, or shorebirds? Were flightless ancestors of today's large flightless ratites (the ostrich in Africa, rheas in South America, emus in Australia, etc.) present on the three southern continents before they separated by continental drift many millions of years ago? The chapters in parts III and IV on behavior and the final chapter on speciation, where Gill is closest to his own area of interest, are especially well done. In these sections he discusses what can be learned from the comparative study of mating systems, kinship in social groups, physiological correlates of behavioral differences among individuals, and the experimental study of the development of song. The only areas that may be missed by today's students are some parts of avian ecology and conservation. I could not find Joseph Grinnell or Evelyn Hutchinson, the concept of the ecological niche, analyses of large-scale trends in populations of waterfowl or landbirds, or much on wildlife management, even of endangered species. But neither could I find areas that could have been sacrificed to make room for these subjects.

Overall, Frank Gill's maturity as a scientist and his appreciation of the beauty and the abilities of birds have enabled him to present a staggering amount of material in an engaging and dynamic manner. I think reading "Ornithology" would enrich the life of anyone with a serious interest in the subject, and I am glad to say that I think that audience has been increasing exponentially in the last few years.—Frances C. James.

Life of the Tanager. By Alexander F. Skutch, illus. by Dana Gardner. Cornell University Press, Ithaca, New York. 1989: 114 pp., 24 color plates, 19 line drawings, 4 tables. $36.50.—Alexander Skutch has compiled many observations on tanagers, mainly from his own fieldwork in Costa Rica, into a nicely illustrated volume that seems to target as its audience the growing number of birder-naturalists who visit the tropics. The well-written, non-technical text is organized into 12 chapters: (1) "The Tanager Family," an overview of the diversity of colors and shapes in the family; (2) "Food and Foraging," which emphasizes the role of tanagers in dispersing fruit; (3) "Voice," (4) "Daily Life," which covers mainly sociality, preening, anting, mobbing, and roosting; (5) "Displays and Disputes," nine pages of anecdotes concerning "quarrels"; (6) "Temperament," which covers wariness of humans and unfamiliar objects; (7) "Courtship and Nests"; (8) "Eggs and Incubation"; (9) "Nestlings and their Care," which includes some excellent descriptions of day-by-day growth of nestlings; (10) "Helpers" (at the nest); (11) "Enemies," which includes an informative tabulation of nesting success; and (12) "Tanagers and Man." A bibliography follows the text, although the references are usually not cited directly in the text.

Other reviewers of Skutch's recent books have pointed out that most material included has been recycled from earlier, more technical publications. Others have noted with varying levels of disdain Skutch's often peculiar outlook on nature and his tendency towards anthropomorphic interpretations of behavior. This volume could be criticized on these grounds as well. I only hope that all those "bad" snakes that Skutch has killed through the years have at least been preserved as scientific specimens. My only major disappointment with the text was that it did not adequately convey the spectacular nature of the mixed-species flocks of gaudy, gleaming tropical tanagers that provide visitors from temperate latitudes with their most indelible, heart-throbbing tropical memories.

So what's in it for the ornithologist? I confess that I was entertained by the anecdotes, some of which are hilarious, others macabre. Some of my favorites include: (1) the female Tropical Gnatcatcher (*Polioptila plumbea*) that ignored its own mate, which was building a nest, to care for nestlings of a pair of Golden-masked Tanagers (*Tangara larvata*) that it tried to drive off; (2) the Scarlet-rumped Tanagers (*Ramphocelus passerinii*) that scolded

shoes hidden in a thicket from marauding mercenary soldiers; (3) the two female Blue-gray Tanagers (*Thraupis episcopus*) that shared incubation duties of a four-egg clutch; (4) the American Swallow-tailed Kite (*Elanoides forficatus*) that seized a tanager nest in flight and carried it and its nestling occupants upwards into the sky; and (5) the Green Honeycreepers (*Chlorophanes spiza*) that reveal their nasty habits at his feeding station. My favorite quotes are: "Some male birds have trouble finding the nest" ("big surprise," says my wife, with great smugness) and "Sometimes birds continue for days to bring food to nests from which they have lost their young." On the other hand, there are just some things about tanagers I'd rather *not* know: ". . . nestlings turn to present their rear ends, from which oozes a gelatinous or watery stuff . . . , which the parent eats little by little, appearing almost to lick it up with its tongue."

Dana Gardner's artwork complements the text nicely. His interesting compositions and brilliant colors counterbalance the somewhat porcelain-like birds. The only mistakes that I noticed were the labelling of the Black-faced Tanager (*Schistochlamys melanopis*) as a "male" (it is monomorphic; the immatures are frequently assumed to be females) and the placement of the arboreal White-rumped Tanager (*Cypsnagra hirundinacea*) on the ground.

If one wants a comprehensive book on the biology of tanagers, then buy Mort and Phyllis Islers' "The Tanagers" (1987, Smithsonian Inst. Press), a scholarly monograph that compiles virtually every bit of information available for all 242 species. If one wants pleasurable reading with many interesting stories skillfully interwoven to illustrate much about the behaviors of tanagers, and if one seeks inspirational prose that enthusiastically conveys much of the magnetism of tropical birds, then buy Skutch's book.—J. V. Remsen.

Return of the Whooping Crane. By Robin W. Doughty. Univ. of Texas Press. Austin, Texas. 1989: 182 pp., 31 color text figs., 6 maps, 7 tables, 2 appendices. $24.95.—Perhaps no other North American bird better symbolizes the plight of endangered species than does the Whooping Crane (*Grus americana*). From a low of 21 individuals in 1944, the population has slowly increased to a current (spring 1990) level of 141 wild birds, plus an experimental flock and those in captivity. Doughty's book is a very readable account of the trials and tribulations of biologists, conservationists, government agencies, and the general public in their efforts to save the Whooping Crane from extinction.

"Return of the Whooping Crane" is divided into seven chapters which include an introduction, discussion of the winter habitat at Aransas National Wildlife Refuge, Texas, nesting habitat in the Canadian Northwest Territories, radio-tracking activities in the early 1980s, propagation programs at the Patuxent Wildlife Research Center, attempts (many of them frustrating) to establish an experimental flock in Idaho, and finally a conclusions section with some thoughts about the future.

Perhaps the most significant contribution made by this work is the attention given to the details of Whooping Crane ecology on the nesting and wintering areas. A wealth of data exists in the scientific literature on habitat needs, management methods, and management direction for those areas. Doughty has quite handily synthesized that information and presented it in a form that both the scientist and lay person can understand and enjoy.

The color photographs, with two exceptions, are very high quality and do an excellent job of portraying Whooping Cranes and their habitats. Seven high quality, multi-colored maps depict various portions of the range of this species including the daily locations of a radio-marked bird tracked from Canada to Texas.

My only real frustration with this book revolves around the over-kill given to the propagation facilities at Patuxent, and the amount of space devoted to the experimental flock in Idaho. This, I believe, was done at the expense of providing more information on the habitats

(and threats to those habitats) used by the birds while on migration. Captive rearing and the Idaho release program are both "showy" aspects of Whooping Crane recovery which have generated much interest in the Whooping Crane. However, little information is provided about migrational habitat other than that obtained from the controversial radio-tracking studies conducted in the early 1980s. There are five federally designated areas of critical habitat for Whooping Cranes in the United States; four of them are migration stopover areas. Discussion of critical habitat is limited to about three paragraphs in the conclusion section, and the bulk of that discussion deals with issues on the winter habitat at Aransas National Wildlife Refuge.

The text is remarkably free of errors, although the publication date for one of my papers in the bibliography was cited as twenty years before the actual publication date. The bibliography contains 287 titles, including scientific papers and various agency reports. This alone is a valuable contribution to the understanding of Whooping Crane ecology.

Although the book does not cover some aspects of Whooping Crane recovery that I believe should have received more space, this book is highly recommended. Doughty's work was designed as an update to McNulty's 1966 publication, "The Whooping Crane: the Bird that Defies Extinction." Because of the multitude of advances in our understanding of Whooping Crane biology since McNulty, Doughty's update was necessary in order to summarize the current state of knowledge. My only hope is that the next update twenty years from now will be titled something like "Recovery of The Whooping Crane." The current title will serve as an essential base for evaluating future efforts to recover the Whooping Crane.—Craig A. Faanes.

Disease and Threatened Birds. Edited by John E. Cooper. International Council for Bird Preservation, Technical Publication No. 10. U.K. 1989: 200 pp. 16 figures, 19 tables, 24 black-and-white photos. A collection of 14 papers by 23 authors presented at the XIX World Conference of the ICBP, June 1986, Queens University, Kingston, Ontario, Canada. Paper. ISBN 0-946888-18-13. £16.50.—While the influence of disease on population dynamics of free-living birds has not weighed heavily in the investigations of biologists, the dire nature and intensity with which endangered and threatened species of birds are being managed approaches the mode of operation of modern poultry operations. Predicted rates of extinction over the next decade forecast an increasing spiral in this trend. Given the importance of disease recognition and control in the poultry industry, one readily concludes that similar concerns should be addressed by those charged with the responsibility for managing endangered and threatened avian species.

This book, edited by one of the world's great advocates for application of veterinary principles to the management of wild birds, adeptly serves as a primer for scientists who, although familiar with the conservation biology of a species, are untrained in assessing the impact of disease processes. The first several papers review the ecology of avian pathogens and the various methods the poultry industry has devised for managing these. Accordingly, the reader is informed that disease can be dealt with by exclusion, elimination or control by vaccination, environmental management and chemotherapy. As ensuing papers indicate, most endangered species in captivity are presently relatively free of pathogens. Given the millions of dollars and decades of time spent by the poultry industry to eliminate troublesome pathogens, such as *Mycoplasma* (sp.) and *Salmonella* (sp.), as well as the annual expenditures for control of coccidia, it is clear that every effort to continue to exclude pathogens from endangered species is the most desirable route.

The basis for concern about diseases in small populations is established in a paper by J. E. Cooper where the combined effects of genetic impoverishment, exposure of naive indi-

viduals or populations to exotic pathogens and the stress of captivity create a situation ripe for exploitation by pathogens and opportunistic organisms. The concern extends also to the potential, but as yet undocumented effects, that could arise wherein captive-produced and released individuals, upon having been rendered carriers of a pathogen in captivity, could upon release to the wild, expose wild birds to a novel pathogen. Indeed, the possibility for dissemination of pathogens by birds is addressed in a chapter which documents introduction of avian influenza by migrating shore birds.

Two situations where exposure of naive populations to a pathogen apparently occurred are provided. The first is an outbreak of Eastern Equine Encephalitis (EEE), an insect-borne viral infection in Whooping Crane (*Grus americana*) at a captive propagation site. Losses of adult breeding birds were significant, and rapid diagnosis required application of a multidisciplinary, technologically sophisticated approach. While control by vaccination of the captive birds was achieved, the event caused re-evaluation of proposed sites in the wild for establishing founder flocks of cranes. In the second case, strong evidence for the role played by introduced pathogens in the demise of the Hawaiian Crow (*Corvus hawaiiensis*) is presented, implicating both avian pox and malaria. These two case profiles are complimented by other papers examining diseases in free-living Australian birds and providing a perspective on the impact of the ubiquitously distributed avian hematozoa. Clearly, the concern for diseases must go beyond the walls of the captive propagation facility.

The text is amply complemented throughout with tables, graphs, line drawings and black-and-white photographs. The multidisciplinary collaborative approach advocated by the editor is facilitated by an appendix which contains a registry of individuals and laboratories throughout the world available for consulting work in wildlife diseases. A second appendix briefly presents screening protocols and post mortem procedures.

Now, who should read this book? I think it pertains to a broad and diverse audience. Biologists, technicians, and managers of endangered and threatened species for whom concepts of pathogen dynamics are not their native tongue, should have this on their must read list. Veterinarians will find it a useful collection of information and will enjoy comparing the information with their own experiences and approaches. Researchers will rejoice at the many situations that are described as being in need of further research. And on that account, perhaps those operating in the rarified atmospheres of agencies and granting institutions which allocate funds should read it also.—Patrick T. Redig.

The Hummingbird Book. By Donald and Lillian Stokes. Little, Brown and Company, Boston. 1989: 96 pp., 70 color photographs, 8 range maps. $9.95.—Hummingbirds are big these days, so it is no surprise that yet another book on the subject has come out.

The Stokes' book fills the "how-to" niche that has been almost completely void. Billed as the complete guide to attracting, identifying, and enjoying hummingbirds, this book comes close to living up to expectations. An initial section on feeders covers types, selection, placement, and number. Additional sections discuss feeding mixtures, maintenance, and feeder problems. These pages introduce the basic concepts of hummingbird feeding for the experienced and beginner alike. A special section on attracting orioles is a nice addition, but it would have been better placed farther from the front of the book.

Since hummingbirds feed on nectar and pollinate many flowers, the sections on habitat are especially valuable. Lists of hummingbird wildflowers of the West and of the East make no claim to completeness yet get the point across that the birds and flowers belong together. The strategy of hummingbird gardening is well discussed in the section by that name although the accompanying plant list contains several species which seem to contain little nectar and

therefore provide only color rather than sustenance. A novice hummingbirder could easily go astray with this list.

The authors have included numerous pages of assorted hummingbird biology and trivia that enable the non-biologist to understand quite a bit about this large family. A section entitled "Photographing Hummingbirds" by Sid Rucker leads one to believe that anyone with a good camera can take good photographs of these agile birds. It fails to mention that most portrait shots are taken of captive birds, a technique beyond the reach of anyone lacking appropriate permits. Two pages of identification notes are primarily useful for identifying males in their breeding regions.

The last half of the book is taken up with species accounts of those species which occur in North America. Each of the eight species with wide distribution is allotted four pages. Range maps show a broad picture of the breeding areas and, in most cases, the wintering grounds. Diagrams of "dive displays" for each species depict the distinctive aggressive displays of each species. A "quick guide" box for each species gives breeding period, migration times, breeding range, and non-breeding range in a brief capsule. Species that have small ranges within the U.S., or that occur irregularly are equitably allotted a single page. A list of resources at the end makes no claim to completeness, but it should have included all of the commonly used field guides for North American birds.

Many attractive photographs add to this book's appeal. For the most part, they are excellent. Although I have a personal preference for "natural" pictures, "studio" shots go far in allowing the reader a clear, unobstructed view. A few of the photos ring less than true. Two female *Selasphorus* misidentified as Black-chinned Hummingbirds on page 7 seem to be the same birds as two Rufous Hummingbirds on page 79. How did they get two hummers to perch next to each other? The adult male Calliope Hummingbird displaying on page 41 has the white-tipped rectrices of an immature. I didn't know that a male could reach breeding condition without molting his original tail feathers.

My major criticism is their failure to capitalize the common names of each bird species, except those that include proper names, and are therefore already capitalized. Lacking capitals, descriptive names seem less like names of species than just generic birds. A zealous nit-picker would list other faults but I shall refrain. This book's value is to the backyard birder or enthusiastic nature lover, and for them, the book is very good.—Nancy L. Newfield.

The Birds of Ohio. By Bruce G. Peterjohn, illus. by William Zimmerman. Indiana Univ. Press, Bloomington, Indiana. 1989: 237 pp., 50 color plates with captioned figs., two maps. $50.00.—The appearance of a major new state bird book is always good news for birders and research ornithologists alike. At their best, these treatises pull together a wealth of information on the distribution, migration, historical trends, and habitat associations for each of the species covered. New insights about avian behavior or ecology may also be distributed liberally throughout the species accounts. The "Birds of Ohio" clearly falls in this category; it is an authoritative and insightful review, the first for Ohio in nearly a century.

Peterjohn begins with a short, six page introduction devoted mainly to defining terms. The species accounts occupy the rest of the book. Most begin with an introductory paragraph presenting a short vignette of the species, describing some interesting aspect of its behavior or ecology, or commenting on historical trends in its status. Abundance throughout the year, by region of the state when appropriate, is then described in detail. Unusually large counts are mentioned, but normal levels of abundance are emphasized. Frequent use is made of

"daily totals" to describe abundance (e.g., "daily totals seldom exceed 3–6"). Detailed accounts of historical trends in abundance, often stretching back to the mid-1800s, are provided for many species (those whose abundance has changed?). The book concludes with a list of references (526 entries) and an index. A series of full-page paintings by William Zimmerman and a single painting by Ohio artist John Ruthven are also included.

This work has three impressive strengths. First, as noted above, the chronologies of the annual cycle are extremely detailed. Arrival times in southern, central, and northern Ohio are reported, overflights are distinguished from the arrival of residents, and the probable causes of unusually large or early flights are discussed. Similar detail is provided for fall migration, and for residents, average dates of laying, hatch, and nest departure are provided Abundance during many of the periods is also reported. This information will enable anyone to determine whether their sightings in the field are typical, unusual, or improbable.

Second, the historical information has been summarized and presented in an interesting and valuable manner. Ohio has a detailed record of avian trends. The first comprehensive account, by Dr. Jared Kirtland, appeared in 1830, and subsequent statewide accounts were published in 1882 and 1903. Numerous regional accounts, especially Trautman's classic "Birds of Buckeye Lake" (1940), have provided detailed information on population trends in this century.

Peterjohn has obviously mastered this imposing body of knowledge. He writes easily and confidently of ups and downs in avian abundance during the past 160 years. Those who view avian populations as rather static, changing little in abundance from decade to decade, would do well to browse through "The Birds of Ohio." For example, among 24 species accounts, spaced evenly throughout the book, I found four species that have generally increased, five that have generally decreased, and four that have both increased and decreased since the mid-1800s. One species was reported not to have changed substantially in abundance since about 1800, and no trend information was given for nine species. Thus, for more than half of the species, pronounced changes in abundance have occurred in the past 160 years. These descriptions of historical trends in abundance should be of interest to many ornithologists, not just those with specific interests in Ohio birds.

The third strength of Peterjohn's book is that it is laced with insightful comments and ideas about the species he describes. For example, many readers will be interested to learn that Common Ravens (*Corvus corax*) "were probably the most numerous corvid in Ohio when the state was first settled," and that documentation of Ivory-billed Woodpeckers (*Campephilus principalis*) in Ohio from archaeological sites must be based on leg bones or other body parts, not on the bill, head, or wings "since they were prized by Indians and actively traded between tribes." Peterjohn frequently discounts early or late records pointing out that they were probably mis-identifications. These remarks should serve as useful cautions for field observers. The author also includes numerous comments about habitat preferences that will interest specialists as well as birders.

My biggest regret about "The Birds of Ohio" is that no syntheses are included. The detailed species accounts could have been used to address numerous issues, such as the following: How have woodland, grassland, scrubland, and wetland birds changed in abundance during the past few decades? Which species are most affected by hard winters, and how fast do they recover? How long have species reduced by market hunting taken to recover? Have area-sensitive or neotropical migrants declined more than other species? It is certainly the author's prerogative to decide that such issues are outside the scope of his book, but I think "The Birds of Ohio" would have been more interesting if a few analyses—perhaps emphasizing conservation issues—had been included. I was also sorry that little use of Breeding Bird Survey data from Ohio was made. The data are easy to obtain and show many temporal and spatial trends clearly. Zimmerman's plates, while attractive, are not, in my opinion,

outstanding, and most have already appeared in "The Birds of Illinois." It is unfortunate that the Indiana Univ. Press did not commission a new set of plates, especially considering the large number of excellent bird artists currently available for such a project.

In summary, "The Birds of Ohio" is a detailed and authoritative account, emphasizing abundance and distribution both at present and since the mid-1800s. It will certainly be *the* book of Ohio birds for years to come, and should be of interest to all ornithologists concerned with temporal trends in avian populations as well as to anyone interested in birds or birding in Ohio.—Jonathan Bart.

The American Crow and the Common Raven. By Lawrence Kilham, illustrated by Joan Waltermire. Texas A&M Univ. Press, College Station, Texas. 1989: 255 pp., Appendix of Scientific Names, 17 numbered figs., 8 tables. $29.50.—Lawrence Kilham absolutely loves corvids. This book is obviously a labor of love about the behaviors of crows which is divided into four unequal sections. The first two parts provide detailed descriptions of his observations of the behaviors of wild American Crows (*Corvus brachyrhynchos*) both in Florida and New Hampshire. The second section concludes with Dr. Kilham's notes and remembrances of hand-raising a crow, "Crowsy." The third part of the book is a rather rambling description of crow behavior in general which speculates on some possible evolutionary origins, associations, and aspects of crow social systems. Part four of the book concerns Common Ravens (*C. corax*) in the wild and the hand-raising of a young crippled Raven, "Raveny."

There are several chapters associated with each section. Each chapter is comprised of very detailed qualitative descriptions of the observations Dr. Kilham made concerning particular aspects of behaviors (e.g., varieties of foraging), and then a discussion in which the author, with a liberal use of literature citations, draws analogies to similar behaviors in other corvids, other avians, and perhaps other vertebrates, which usually includes wolves (*Canis lupus*) and humans (*Homo sapiens*). It is in these discussion sections that Dr. Kilham's scientific background is demonstrated, and also these areas that form the basis for a fatal flaw in the book. This flaw may lead the casual reader and the dedicated amateur to incorrectly conclude that she/he is reading scientific literature.

The preface of the book tells the reader that statistics are not necessarily useful in trying to understand animals. Yet in each discussion section strong evolutionary correlations are drawn between the crow or raven behavior and similar behaviors in other organisms. I suggest that venturing such relationships demands the use of some statistical support. To suggest the notion that avian behavior has a peculiar place in science that does not rely on statistics does not give proper legitimacy to the field.

To the professional ornithologist, the descriptions of the behaviors have little meaning. There is no flow. There is little context. There is not nearly the amount of quantitative detail to allow the descriptions to be useful. For example, Chapter 4 (Territory and Food Storing), begins with a brief description of 47 territorial encounters between 1981 and 1983. The description references a pen and ink drawing which adds no detail nor clarity to the description. To have some value, the professional ornithologist needs to have some idea of the length of each encounter, the behaviors of each of the participants and the periodicity of the encounters (time of year, time of day, period since the last encounter etc.) for the description. I fear an amateur might find this description engaging and then mistakenly infer that it is a scientific observation due to the detail and scientific context of the writing.

Throughout the book, the behavioral descriptions are liberally laced with anthropomorphic terminology (e.g., use of weapons, fooling, small talk, respect, etc.). Although a non-

scientific book could make such depictions, the overriding tone of this book suggests that anthropomorphic descriptions are scientifically permitted.

In summary, I can not determine who should read this book. It is not one that should be on the professional shelf of an ornithologist. The amateur must be wary of the book also. It has a prevailing style of scientific veracity which may deceive the unsuspecting amateur into the pitfalls that field biologists and behaviorists have been successfully climbing out of for the last dozen years.—Richard B. Stiehl.

Birds of the Canadian Rockies. By George W. Scotter, Tom J. Ulrich, and Edgar T. Jones. Western Producer Prairie Books, Saskatoon, Saskatchewan. 1990: xvi + 170 pp., four black-and-white drawings, many color photographs. $22.95.—Anyone who has experience in birding in the northern Rocky Mountains probably has seen a copy of Ulrich's "Birds of the Northern Rockies." The present book is very similar to that text. It presents the birds of the Canadian Rockies through a series of color photos accompanied by descriptive paragraphs. One might ask why a second book was necessary, given the similarity of the coverage format (several photos seems to be the same in both books). Additionally, one might also wonder why the present book, similar in size to "Birds of the Northern Rockies," costs nearly three times as much. "Birds of the Canadian Rockies" does cover areas not included in the scope of the northern Rockies book, but there is considerable overlap of the avifauna in each.

"Birds of the Canadian Rockies" is an attractive book and is relatively free from typographic errors. The pictures generally are clear and helpful, although some appear to be of birds in captivity. Both the Downy Woodpecker (*Picoides pubescens*) and the Hairy Woodpecker (*P. villosus*) photos show the birds in virtually the same position on the same perch! The authors occasionally point out interesting facts about distribution or habitat selection of selected species, but this part of the book could have been much stronger.

A few things are disturbing about the book. Although it purports to be a field guide, it is of little use in identifying some birds. For example, the authors say only God can separate Hammond's Flycatchers (*Empidonax hammondii*) from Dusky Flycatchers (*E. oberholseri*) in the field. They also do not recognize the division of the Western Flycatcher into two species, the Pacific-slope Flycatcher (*E. difficilis*) and the Cordilleran Flycatcher (*E. occidentalis*). For my taste, too many "throw-away" words are used in the descriptions of birds in this book. These include the frequent use of words such as "odd-looking," "handsome," "busybody," "elegant," "boisterous," and others. The coverage of each species is uneven. As many as three different photos are presented for species that have little plumage variation and are easy to identify (e.g., American Dipper [*Cinclus mexicanus*]). Others are pictured only once and some not at all. Photos of sexually dimorphic species sometimes include females, but there are several notable omissions (e.g., Yellow-headed Blackbird [*Xanthocephalus xanthocephalus*], Red-winged Blackbird [*Agelaius phoeniceus*], Red Crossbill [*Loxia curvirostra*]). Diet, song, and plumage variation are given for some species and omitted for others.

All-in-all, the book will be popular with the casual visitor to the northern Rockies, but will not be of much use to an experienced ornithologist, and I hope that beginning birders buy a copy of one of the standard North American field guides before they obtain this one.—Charles R. Blem.

VOICES OF THE NEW WORLD PIGEONS AND DOVES, ORDER COLUMBIFORMES, FAMILY COLUMBIDAE. By J. W. Hardy, G. B. Reynard, and B. B. Coffey, Jr. ARA Records, P.O. Box 12347, Gainesville, Florida 1989. Monaural tape/casette, $10.50.—In this casette tape, the authors have brought together the voices of 61 of the 70 species of columbiforms known to breed in the New World. These include fifty-seven native and four introduced species from the Old World. With few exceptions, the cuts retain the high quality of recording of all previous ARA productions.

Columbids are marvelous subjects for the study of evolution of behavior as their bowing displays (or the homologs) are innate, so that morphologically similar species often have very similar displays which may be useful in understanding relationships (Goodwin, Auk 83:117–123, 1966; Frith, H. S., Pigeons and Doves of Australia, Rigby Publishing, Adelaide, 1982). The cross-fostering and hybridizing experiments by Whitman, Lade, and Thorpe have revealed that the voices of pigeons are also innate (e.g., Lade and Thorpe, Nature 202: 366–368, 1964). These recordings enable the listener to test whether the evolution of voices also parallels changes in morphology. One sees that in most cases they do, e.g., the morphologically similar *Columba leucocephala* and *C. squamosa* have strikingly similar songs.

When the songs and displays are not similar in taxa considered to be close relatives, is it because voice has evolved independently of morphology or is it because the relationships of those taxa need closer scrutiny? For example, *Zenaida macroura, Z. aurita, Z. auriculata,* and *Z. graysoni* have very similar displays and songs, but *Z. asiatica* and *Z. galapagoensis* do not. Are these taxa correctly treated as congenerics?

In the notes accompanying the tape, the authors inform us that when they designate a sound as "song" they are referring to the advertising song. However, the recordings of the Rock Dove (*Columba livia*) are those delivered during its bow-coo (or display coo). In contrast to the relatively complex songs of the New World *Columba* species, the advertising song of *C. livia* is a simple one note coo repeated in series (Baptista and Abs, Vocalizations, *In* Physiology and Behavior of the Pigeon, M. Abs (ed.), Academic Press, pp. 309–325, 1983).

Although, as pointed out by Hardy et al., New World *Columba* "growl" in aggressive contexts, they also use a "growl" sound as an alternate to the advertising coo or during the nest demonstration display (see e.g., Goodwin; Condor 66:418–422, 1964).

Song repertoire in most pigeons and doves is usually quite small: one or two advertising songs and a nest-display song. The advertising song may sometimes double as the bow-coo song. The Croaking Ground-Dove (*Columbina cruziana*) has an exceptionally large song repertoire. Although Hardy et al. present two song variations in the tape, Trollope (Avicul. Mag. 80:181–188, 1974) reports that it utters a distinct nest-calling song plus four "variations" of the advertising song. There is also marked sexual dimorphism in vocalizations. This species deserves a closer look.

None of my remarks is meant as serious criticism of what is an outstanding compendium of the songs of New World pigeons and doves. The flute-like songs of doves may be enjoyed for their beauty alone; additionally, as developed above, these songs may be used as taxonomic tools to understand better the relationships between taxa.

In addition to the advertising songs of the nine taxa not yet recorded, this reader hopes that recordists will also make an effort to record the nest-display songs of all the species, as these sounds will probably also prove useful to taxonomists. For example, a number of authors have suggested that New and Old World *Columba* are not close relatives (review in Ingold et al. Comp. Biochem. Physiol. 77:427–430, 1984). Hardy et al. present the nest-display songs ("growls") of 11 of the 17 New World *Columba* species. Sound spectrograms of these and a twelfth species from my collection (*C. squamosa*) are structurally quite similar, and may well prove a useful character in distinguishing the New and Old World forms.—LUIS F. BAPTISTA.

Wilson Bull., 103(1), 1991, pp. 162–163

Short Reviews

Current Topics in Avian Biology. Edited by R. van den Elzen, K.-L Schuchman, and K. Schmidt-Koenig. Deutsche Ornithologen-Gesellschaft, Bonn. 1990: viii + 403 pp., many black-and-white figures. No price given.—In honor of the centennial meeting of the Deutsche Ornithologen-Gesellschaft, an international Conference was held in Bonn in September 1988. At hand is a collection of 53 papers (of which 24 are in English, the remainder in German with English abstracts) given at that conference. Thirteen of the papers come under the heading of Biogeography and Systematics, with History of Bird Faunas, Morphology, Species Concepts, Faunas and Exchange of Faunal Elements, and Studies of Relationships as subtopics. The remainder are grouped as Behavioral Ecology, which includes Bioacoustics, Ecology of Marine Birds, Telemetry, Control of Bird Migration, Population Biology Mating Systems, Homing and Orientation, Foraging Strategies, Ecomorphology and Habitat Selection, Comparative Aspects, and Circannual Periodics. The papers by and large do represent the cutting edge of ornithology, but as is usual with symposia, the papers vary from detailed to brief and from ones that are stimulating to others which are rehashes of earlier publications. Although several Americans participated in the symposium only three papers deal with North American birds.—G.A.H.

Monitoring Bird Populations in Varying Environments. Annales Zoologici Fennici. Vol. 26, no. 3. Edited by Yrjö Haila, Olli Järvinen & Pertti Koskimies. Finnish Zoological Publishing Board, Helsinki, Finland. 1989: 181 pp., many black-and-white graphs and maps. No price given.—The papers, given at the 10th International conference on bird census work and atlas studies held at Helsinki in August 1987, constitute a full issue of *Annales Zoologici Fennici*. There are 22 papers together with an overview by P. Koskimies. Most of the papers are by Finnish workers but nine other countries were represented. The papers are organized into four general topics: Methodological (7 papers); The Population Level (5 papers); The Community Level (5 papers) and The Biogeographical Level (5 papers). The first and last sections will be of most interest to American readers.—G.A.H.

The Practical Ornithologist. By John Gooders., Scott Weidensaul (ed.), photgraphs by Bruce Coleman. Simon and Schuster, Inc., New York. 1990: 160 pp., many color and black-and-white photos. $14.95. (paper).—This is an attractive handbook for beginning bird watchers. There are chapters on elementary bird biology, bird behavior, and on the birds expected in seven distinctive habitat situations. A chapter discussing binoculars, field guides and other birding techniques is the central chapter. The last chapter is entitled "From Birder to Ornithologist." The whole is profusely illustrated with first-class color photos, well reproduced. The editor has done a good job of converting what must have been originally a British book for use by American birders, but its ancestry shows through. Wilson Society members will find little of value here, but it might make a good present for a novice acquaintance or an eager youngster.—G.A.H.

An Introduction to New England Birds. (Revised edition) By Christopher Healy, illus. by N. W. Cusa. Massachusetts Audubon Society, Lincoln, Massachusetts. 1989: 32 pp., seven color plates. (No price given).—This attractive little brochure was part of the registration packet at the 1990 Annual Meeting. It presents short essays on seven typical birding situations (Suburban Birds, Summer Woodland, Winter Feeder, etc.). Each essay is illustrated by a composite color painting showing up to 12–14 species. The text is factual and authoritative and the paintings adequate.—G.A.H.

Nesting Ecology of Golden Eagles and Other Raptors in Southeastern Montana and Northern Wyoming. By Robert L. Phillips, Anne H. Wheeler, J. Michael Lockhart,

Terrence P. McEneaney and Nick C. Forester. Fish and Wildlife Technical Report 26. U.S. Fish and Wildlife Service, Washington. 1990: v + 13 pp., 5 black-and-white photos, two graphs and one map. (Free).

Distribution and Abundance of Golden Eagles and Other Raptors in Campbell and Converse Counties, Wyoming. By Robert L. Phillips and Alan E. Beske. Fish and Wildlife Technical Report 27. U.S. Fish and Wildlife Service, Washington., 1990: 31 pp., 18 black-and-white photos, six maps, five graphs. (Free).—These two Technical Reports are bound together and are obtainable from the Publications Unit, U.S.F.&W.S., 18th and C Streets, Mail Stop 1111, Room 130, Arlington Square Building, Washington, DC 20240.—G.A.H.

INFORMATION FOR AUTHORS

The Wilson Bulletin publishes significant research and review articles in the field of ornithology. Mss are accepted for review with the understanding that the same or similar work has not been and will not be published nor is presently submitted elsewhere, that all persons listed as authors have given their approval for submission of the ms, and that any person cited as a personal communication has approved such citation. All mss should be submitted directly to the Editor.

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Style and format.—The current issue of *The Wilson Bulletin* should be used as a guide for preparing your ms; all mss must be submitted in that format. For general matters of style authors should consult the "CBE Style Manual," 5th ed., Council of Biology Editors, Inc., Bethesda, MD, 1983. Do not use footnotes or more than two levels of subject subheadings. Except in rare circumstances, major papers should be preceded by an abstract, not to exceed 5% of the length of the ms. Abstracts should be informative rather than indicative, and should be capable of standing by themselves. Most units should be metric, and compound units should be in one-line form (i.e., $cm\text{-}sec^{-2}$). The continental system of dating (19 Jan. 1950) and the 24 hour clock (09:00, 22:00) should be used.

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The editor welcomes queries concerning style and format during your preparation of mss for submission to the *Bulletin.*—Charles R. Blem, Editor.

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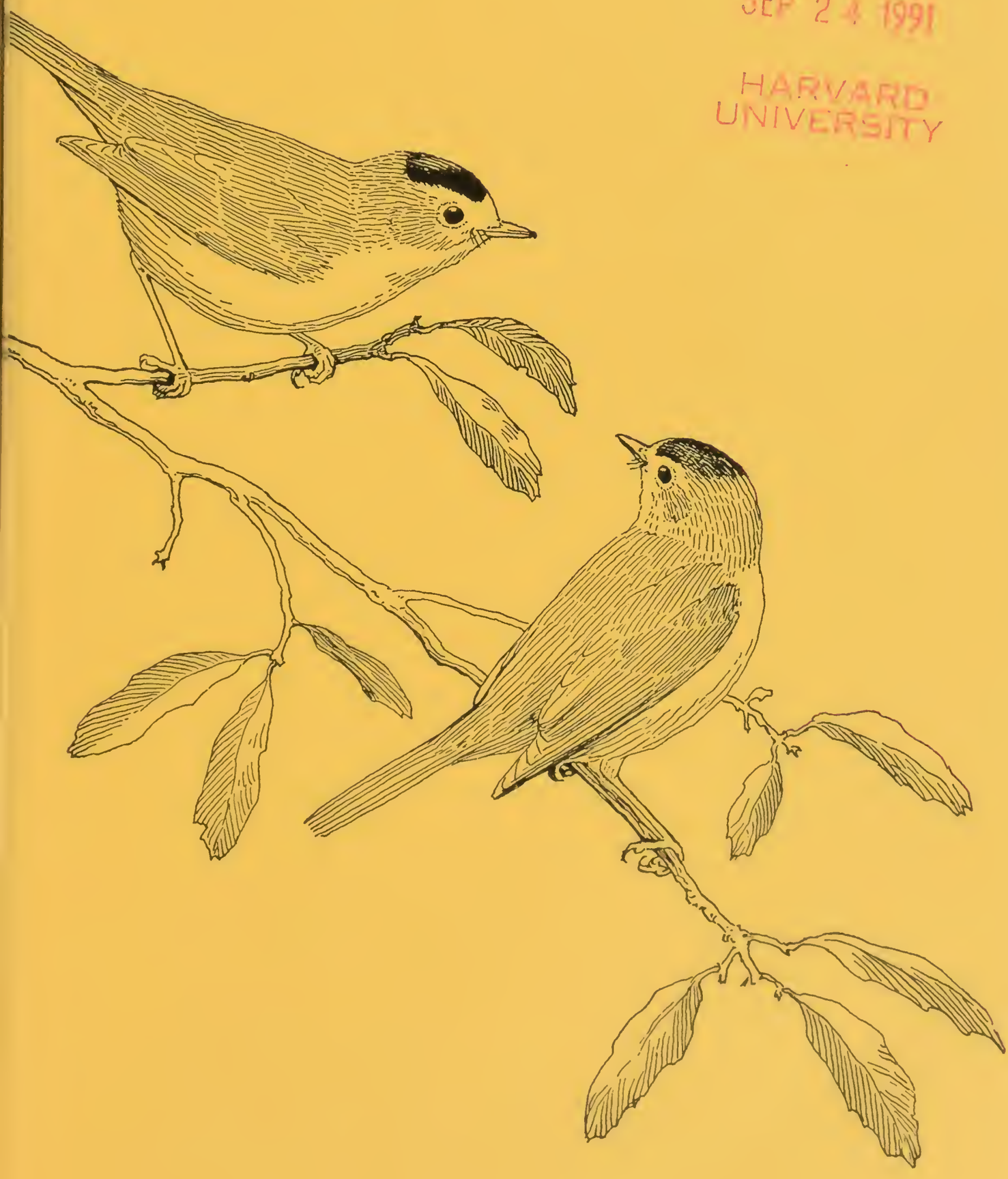

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POPULATION TRENDS OF SOME NORTHEASTERN NORTH AMERICAN LANDBIRDS: A HALF-CENTURY OF DATA

NORMAN P. HILL[1] AND JOHN M. HAGAN, III[2]

ABSTRACT.—We analyzed population trends of 26 species of North American migratory landbirds using 53 years of spring migration count data collected in eastern Massachusetts from 1937 to 1989, inclusive. These data span twice the time period of most landbird monitoring data sets, allowing us to examine how accurately trends based on shorter-term investigations of population trends represent longer ones. We found that 18 species (64%) have declined significantly, three species (12%) have increased significantly, and five species (19%) have shown no trend over this time period. Using the most recent ten years of our data, the trend matched that of the full 53-year data set for 10 species (38%). Using the most recent 20 years of data, the number of matching trends increased to 18 (69%). Using a 30-year subset of data did not improve the percentage of matching trends and showed a greater number of non-significant trends than did analysis of the most recent 20-year subset of data. This pattern resulted because many species appeared to be at low population levels in the 1950s and early 1960s, before the time when most current avian censuses and surveys began. Our results indicate that many species are in fact declining, but that declines in the past 20 years might be partly a result of normal, shorter-term population fluctuations. *Received 24 Aug. 1990, accepted 28 Nov. 1990.*

There is increasing concern that populations of many North American migrant bird species are declining (Robbins et al. 1989, and see review in Askins et al. 1990). Because of the relatively restricted winter ranges of many Neotropical migrant species (Rappole et al. 1983), the habitat specificity of some, and the recently accelerated rate of tropical deforestation (cf. Gradwohl and Greenberg 1988), concern has centered on those species that breed in North America but winter in Central or South Amer-

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The Variable Screech-Owl (*Otus atricapillus*) and its relatives. See special ornithological literature review by Marshall, Behrstock and Konig, p. 311. Painting by Joe T. Marshall.

ica (e.g., Terborgh 1989). Effects on breeding season biology imposed by forest fragmentation in North America have also been implicated in causing declines in these species (e.g., Whitcomb 1977, Whitcomb, B. L. et al. 1977, Whitcomb, R. F. et al. 1981, Robbins 1980, Lynch and Whigham 1984, Askins and Philbrick 1987, Askins and Sugeno 1987). Reproductive success of many forest-dwelling migrant passerine species is reduced near forest edges as a result of increased predation (Wilcove, 1985a, b; Small and Hunter 1988) and parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Mayfield 1977, Brittingham and Temple 1983). Although the amount of forested land in the eastern United States in recent decades has remained stable, or slightly increased in some areas (Terborgh 1989, Birch, unpubl. data), existing forest has become increasingly fragmented because of roads and urbanization (Terborgh 1989).

Recognizing these major, broad-scaled changes in habitat, researchers have attempted to monitor migrant bird populations in North America so that predictions can be made about future population levels and so that species or species groups of critical concern can be identified. Studies have relied on data from the U.S. Fish and Wildlife Service's Breeding Bird Survey (see Robbins et al. 1986), numerous breeding bird censuses (Johnston and Winnings 1987, Holmes and Sherry 1988), or on migration counts or captures (Hussell 1981, Jones 1986, Stewart 1987, Hagan et al., in press, Hussell et al., in press). Some studies have recently documented declines in some migratory species (e.g., Holmes and Sherry 1988, Robbins et al. 1989), but most are subject to criticism because they are based on only about 20 years of data and therefore might not represent long-term trends. Many bird populations show natural fluctuations at this temporal scale. For example, reproductive success of many warbler species that breed in the boreal forest is substantially increased as a result of spruce budworm (*Choristoneura fumerifana*) outbreaks (Kendeigh 1947, MacArthur 1958, Morse 1978, Harrison 1984), a major food of many migrant passerine warblers during the breeding season. Recent declines reported by some studies might be a consequence of elevated population levels in early and mid-1970s when there was a massive outbreak of the spruce budworm in the northeastern United States and Canada (Hardy et al. 1981). That is, man-induced habitat change in the Neotropics or the Nearctic might not be the cause for recent declines. Unfortunately, data on populations prior to the mid-1960s are rare.

In this paper we analyze population trends of 26 Nearctic-Neotropical migrant landbird species using spring migration census data collected over a 53-year period (1937–1989) in eastern Massachusetts. This data set is unusual in its completeness and duration. It provides an opportunity to examine population changes of some species for over half a century, and

therefore allows us to investigate how accurately trends based on shorter-term data represent longer ones. By using temporal subsets of the full data set, we also estimate how many years of data would have been needed before long-term population trends would have been revealed (those obtained by the full data set), and we show that shorter periods of census data can be misleading.

METHODS

Our data come from the field notes of N. P. Hill and from those of the late Ludlow Griscom (Assistant Curator of Ornithology and Research Ornithologist, Museum of Comparative Zoology, Harvard University). From the 1930s until his death in 1959, Griscom was an acknowledged leader in field ornithology; his notes are currently deposited in the Peabody Museum in Salem, Massachusetts. The raw data are counts of birds seen in the field during spring migration in May in Middlesex and Essex counties in eastern Massachusetts. Specific sites within these counties were visited each year between 1937 and 1989. Middlesex county sites routinely visited included the towns of Cambridge (especially Mt. Auburn cemetery, a well-known "birding" location during migration), Arlington, Belmont, Lexington, Concord, and Wayland. In Essex County, sites were located in a strip of countryside from Lynnfield and Nahant north to West Newbury, Newburyport, and Plum Island. Hill collected data at these sites from 1940–1946, and then from 1952–1989; he was absent from the state from 1947–1951. L. Griscom collected data from 1937–1958, although illness prevented field work by him in 1956. Thus, the two data sets collected in the same locations overlap in the 1950s.

These data were recorded by the observers, mostly on intensive "birding" excursions, often from pre-dawn to after dark. Bird sightings were recorded in field notebooks at the time of sighting, and records of hours of effort were always kept. However, because sampling did not follow a prescribed protocol, several sources of undesirable variation were imposed on annual population estimates. For example, the number of hours spent in the field varied among years. Hill spent from 7–103 h ($\bar{x}$ = 28.8 h, N = 45 years) and Griscom spent from 37–108 h ($\bar{x}$ = 79.3, N = 21 years) per year in the field. Also, which days were spent in the field varied from year to year, although we used only sampling days in May when migration is at a peak in southern New England. No effort was made to be in the field only when certain weather conditions prevailed, and each excursion usually lasted an entire day. Furthermore, because observers were in the field for only a few days each May, migration "fall outs" (migration interrupted by weather or other factors) could cause inflated counts if observers happened to be in the field on those days.

Some effects of these sources of variation can be minimized through analysis. First, to accommodate annual variation in effort, the number of birds of each species seen each May was converted to the number seen per hour of field observation. Because of the high variability in annual counts, partly owing to weather and partly to stochastic features of migration, we calculated population indices using a 5-year moving average. Each of the five years was given equal weight in the calculation of the moving average. Finally, for the purposes of documenting long-term trends, the temporal extent of the data set tended to overcome these sources of variation.

Local environmental and habitat change was not quantified during the study, but some change was evident. There was no general urbanization or major change in wetlands in areas censused, but some loss of agricultural area and some increase in suburban residential area was apparent. Some pastureland was lost to residential growth in the towns of Lexington, Concord, Wayland, Lynnfield, and West Peabody and to industrial growth in the Newbury-

port area. There was a general loss of brush and second-growth habitats, and forests became more fragmented but without a substantial overall loss of area. In some areas, habitat improved with the creation of the Great Meadows Wildlife Refuge in Concord and the Parker River Refuge on Plum Island.

We analyzed population trends of 26 Neotropical migrant species and two temperate, resident species, although for only 14 species did we have both Griscom and Hill data. Data from Griscom's field notes were useful only for this subset of species recorded by Hill because Griscom was primarily interested in uncommon species sightings. He often wrote that numbers were "normal" or that a species was "fairly common." We used his data only for those species in which he recorded the actual number of individuals observed. If Griscom records were available for a species, 53 years of continuous data (49 smoothed points) were available for analysis (1937–1989). With Hill data alone, 38 years of continuous data (34 smoothed points) were available (1952–1989), with an additional seven years of data which were collected from 1940–1946.

To assess population trends over this half-century of time, and to assess how much data might be needed to reveal the same trend as observed for the full data set for each species, we analyzed the trends using only the most recent ten years of data, then the most recent 20, 30, and 40 years, and finally the entire data set. We operationally defined the "long-term" trend for each species as the one revealed by the entire data set. For each increment of data, we performed simple linear regression on the $\log_e$ of the smoothed data points, and used the slope of the regression to calculate a percent annual change during that period, following the methods described by Holmes and Sherry (1988). We used the *P*-value of the regression to determine the significance of population change. Two data points were sacrificed on either end of the regression because of the 5-year smoothing function. We did not include the disjunct data from 1940–1946 collected by Hill in regressions because, after smoothing, it provided only three data points, and without Griscom data to span the gap in the Hill data, these three points could unduly influence the slope and significance of the regression.

A word of caution is warranted concerning regression *P*-values. Using regression to document significant population trends is inherently biased because data points are not independent. For example, two data points close in time are more related than two points far apart in time. A large population in one year can lead to several years of high population indices. Smoothing data can exacerbate this problem. However, smoothing also tends to produce more realistic annual population indices because of the many sources of annual variation in migration counts unrelated to real population change (weather, varying migration routes, etc.). We have sacrificed independence for realism. Smoothing can either enhance or reduce statistical significance; thus, we regard calculated *P*-values as only indices of significance of population change. Because all data were treated identically, lower *P*-values should represent greater significance, albeit inexact representations.

RESULTS

For 12 Neotropical migrant species, 38 years of data were available for analysis and for 14 species, 53 years of data were available (Table 1). Using all data for each species, we found that 18 species (69%) have declined significantly and three species (12%) have increased significantly in numbers (Table 2). Five species (19%) showed no significant change.

Using the most recent ten years of data (smoothed points 1978–1987), trends matched those of the full data set for ten species (38%) (Table 1). Using the most recent 20 years of data, the percent of matching trends

increased to 69%. Using 30 years of data, the percent of trends that matched the full data set (62%) did not improve over the percent observed for the 20-year data subset. For the 12 species with 38 years of data (34 smoothed points), the "40-year" trend was, by definition, correct. For the remaining 14 species with 53 years of data (49 smoothed points), 12 (92%) matched the long-term trend using the 40-year data subset. Trends in 19 of all 26 species (73%) failed to match their long-term trend for at least one time interval.

The 10-year subset of data showed 14 (54%) non-significant trends, whereas the 20-year subset showed only six (23%) (Table 2). The 30-year subset of data showed 14 (54%) non-significant trends, the same as the 10-year subset (Table 2). Plots of population indices for individual species indicate why this pattern was evident (Fig. 1). Population levels of many species were elevated in the 1968–1977 time period, and low in the 1978–1987 period, which caused many significant negative trends (and few non-significant trends) in the last 20 years of data. Populations of many species also tended to be at low levels in the late 1950s and early 1960s. Thus, when we included 1958–1967 data (the 30-year subset), many trends became non-significant, rather than significant, and negative. The last four decades of data combined showed only seven nonsignificant trends, and 17 of the 21 significant trends were negative (Table 2). Thus, the 40-year data set showed many of the negative trends revealed by the shorter, 20-year subset.

Considering both statistically significant and non-significant population trends, the most recent decade of data showed a mean change per year of −2.2%. Using the 20-year data set, the mean annual change was −2.0%. With 30 years of data, the subset that showed many non-significant trends, the mean annual change decreased to −0.86% per year. The mean annual rate of decline increased to −1.1% using the 40-year subset and to −1.2% using all available data (34 smoothed points for 12 species and 49 points for 14 species). The rate of change varied from +0.7% (Bay-breasted Warbler) to −3.8% (Least Flycatcher) (see Table 2).

These results also show a cyclic nature of population change for some species. Visual inspection of the graphs (Fig. 1) reveals information about trends that is difficult to obtain quantitatively. Various patterns in population change are evident, including: (1) cyclic change with no long-term trend, (2) cyclic change with slow overall decline, (3) cyclic change with an overall increase, (4) long, linear decline, and (5) linear increase. Species that showed cyclic trends typically had two or three pronounced peaks in abundance during the entire time span. Consistent long-term declines were found in species with both cyclic and linear patterns of change. We defined a consistent long-term decline as one that showed a significant

TABLE 1

ANNUAL RATE OF POPULATION CHANGE (PERCENT PER YEAR) FOR 28 SPECIES BASED ON 49, 40, 30, 20, AND 10 "SMOOTHED" YEARS OF DATA. THE OVERALL TREND ("TREND" COLUMN) IS BASED ON THE MAXIMUM AVAILABLE DATA FOR A SPECIES

Common name	Scientific name	Trend[b]	Years of data[a]				
			49	40[c]	30	20	10
Least Flycatcher	*Empidonax minimus*	−−	−3.1**	−3.8**	−2.8**	−2.9**	ns
Great Crested Flycatcher	*Myiarchus crinitus*	−	x	−0.9**	ns	ns	+3.2**
Tufted Titmouse	*Parus bicolor*	++	x	+2.6**	+2.8**	+4.3**	+2.5**
Swainson's Thrush	*Catharus ustulatus*	−	−1.6**	−2.0**	ns	ns	ns
Red-eyed Vireo	*Vireo olivaceus*	ns	x	ns	ns	ns	−3.9**
Blue-winged Warbler	*Vermivora pinus*	++	x	+0.5**	+0.6**	+1.0**	+2.1**
Golden-winged Warbler	*V. chrysoptera*	−−	−1.4**	−1.4**	−1.4**	−0.8**	ns
Tennessee Warbler	*V. peregrina*	+	x	+1.6**	+1.3*	ns	ns
Nashville Warbler	*V. ruficapilla*	−−	−1.9**	−2.0**	−1.2**	−0.7*	ns
Northern Parula	*Parula americana*	ns	ns	ns	ns	−4.7**	−7.5**
Chestnut-sided Warbler	*Dendroica pensylvanica*	−−	−1.2**	−1.6**	−1.4**	−2.4**	ns
Magnolia Warbler	*D. magnolia*	−−	−2.4**	−3.2**	−2.6**	−3.6**	ns
Cape May Warbler	*D. tigrina*	−	−0.2*	ns	ns	−1.9**	−1.6**
Black-throated Blue Warbler	*D. caerulescens*	−	−1.0**	−1.3**	ns	−4.5**	ns
Black-throated Green Warbler	*D. virens*	−	x	−1.1*	ns	−2.3*	−8.0**
Blackburnian Warbler	*D. fusca*	ns	x	ns	ns	−2.5**	−2.3*
Bay-breasted Warbler	*D. castanea*	+	+0.7**	ns	ns	−5.0**	ns
Blackpoll Warbler	*D. striata*	−	−1.3**	−1.2**	ns	ns	ns
Black-and-white Warbler	*Mniotilta varia*	−	x	−1.6**	ns	−4.2**	−10.3**
American Redstart	*Setophaga ruticilla*	−	x	−1.7*	ns	−1.7**	ns
Ovenbird	*Seiurus aurocapillus*	−−	x	−2.2**	−1.8**	−3.1**	−7.1**

TABLE 1
CONTINUED

Common name	Scientific name	Trend[b]	Years of data[a]				
			49	40[c]	30	20	10
Northern Waterthrush	*S. noveboracensis*	−−	−0.8**	−0.8**	−0.7**	−1.2**	−1.5**
Wilson's Warbler	*Wilsonia pusilla*	−−	−0.5**	−0.8**	−1.4**	−2.5**	−0.7*
Canada Warbler	*W. canadensis*	−−	−1.5**	−1.8**	−1.8**	−2.2**	−4.0**
Scarlet Tanager	*Piranga olivacea*	ns	x	ns	ns	−3.2**	ns
Northern Cardinal	*Cardinalis cardinalis*	+	x	+3.1**	+3.3**	+3.8**	ns
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	ns	x	ns	ns	ns	ns
Northern Oriole	*Icterus galbula*	−	x	−1.2**	−1.3**	−1.3*	ns

[a] "*" indicates $0.01 > P < 0.05$, and "**" indicates $P < 0.01$ for linear regression model, "ns" indicates no statistical significances, "x" indicates data not available.
[b] "− −" or "+ +" indicates that the same significant trend was detected for at least four time intervals. "−" and "+" indicate that the long-term trend was significantly positive or negative.
[c] Only 34 "smoothed" data points available for 14 species with "x" in "49" year column.

TABLE 2

SUMMARY OF LINEAR REGRESSION ANALYSES ON SUBSETS OF THE SMOOTHED DATA. A TREND WAS DEEMED SIGNIFICANT IF THE *P*-VALUE FOR THE REGRESSION WAS LESS THAN OR EQUAL TO 0.05. THE TWO TEMPERATE RESIDENT SPECIES ARE NOT INCLUDED IN THE TABULATION

Parameter	Number of years					
	All	49[b]	40[c]	30	20	10
Number (+) trends	3	1	2	2	1	2
Number (−) trends	18	12	17	10	19	10
Number n.s. trends	5	1	7	14	6	14
Number matching trends[a]	26	14	24	17	18	10
Percent matching trends[a]	100	100	92	65	69	38
Number species	26	14	26	26	26	26

[a] "Matching" means the same as the trend of the full data set.
[b] Only those species with 49 smoothed years of data.
[c] Only 34 smoothed points for 12 species (see Table 1).

negative slope for at least four of the component regression time periods (see Table 1). Nine species (scientific names in Table 1) showed such declines: Least Flycatcher (Fig. 1a), Golden-winged Warbler (Fig. 1g), Nashville Warbler (Fig. 1i), Chestnut-sided Warbler (Fig. 1k), Magnolia Warbler (Fig. 1l), Ovenbird (Fig. 1u), Northern Waterthrush (Fig. 1v), Wilson's Warbler (Fig. 1w), and Canada Warbler (Fig. 1x). The plot of the Wilson's Warbler trend (Fig. 1w) does not visually convey the long-term pattern of decline indicated by the statistical analysis. The consistent negative slope derived from the successive regression analyses was caused by the very low counts during the last decade, which significantly influenced each regression. Two other species also have shown a notably precipitous decline in the last decade: Black-throated Green Warbler and Black-and-white Warbler. Only one Neotropical migrant species showed a long-term consistent increase (at least four regressions with a significant positive slope): Blue-winged Warbler. The Northern Cardinal and Tufted Titmouse, two resident species, also showed clear increases in numbers (Table 1).

The methods of data collection used in this study were not as standardized as more conventional methods of bird population monitoring, such as the Breeding Birds Survey (Robbins et al. 1986), Breeding Bird Censuses (cf. Askins et al. 1990), or migration captures or counts (Hussell 1981). However, trends of selected species indicate that our data reflect real population changes. The Northern Cardinal and the Tufted Titmouse both showed strong increases in numbers (Fig. 1c and 1z, respectively) that coincided with the well-documented expansion of these two species

into southern New England (Beddall 1963, Laughlin and Kibbe 1985). We also showed that the Blue-winged Warbler (Fig. 1f) steadily increased, while during the same time period the Golden-winged Warbler (Fig. 1g) decreased. The range changes of these two species, presumably because of the more general habitat requirements of the Blue-winged Warbler, is also well-known (Confer and Knapp 1979).

DISCUSSION

The present data set allowed us to distinguish between short-term (<20 years) and very long-term (30–50 years) patterns of population change. For example, Robbins et al. (1989), using data from 1966–1987, reported significant population declines in Neotropical migrants. Using a subset of our data from 1966–1989 (smoothed points 1968–1987), we showed similar trends for the same species. However, by inclusion of data from the decade prior to this time, many of these significant declines became nonsignificant (e.g., see Fig. 1j, Northern Parula; Fig. 1m, Cape May Warbler; Fig. 1n, Black-throated Blue Warbler; Fig. 1o, Black-throated Green Warbler; Fig. 1p, Blackburnian Warbler; Fig. 1q, Bay-breasted Warbler; Fig. 1s, Black-and-white Warbler; Fig. 1t, American Redstart; and Fig. 1y, Scarlet Tanager). This was because the populations of many species appear to have been at low levels prior to the sampling period of Robbins et al. (1989). Thus, some of the declines they reported might have been because of natural downturns in populations after naturally induced population increases in the first decade of their study, rather than declines caused by human-induced habitat loss.

However, our results support the contention that many Neotropical migrant species are declining in abundance. Despite the lack of many trends using our 30-year subset of data, when we used the entire data set most of the significant negative trends reappeared that were revealed with the shorter-duration subsets of data (see Table 1). Negative trends for some species with high population levels in the 1970s and low levels in the 1980s "happened" to correlate with the full data set because the long-term pattern of change was also negative. However, the mechanisms which caused these two negative trends were probably different. If the species that showed cyclical patterns of change had been entering a phase of natural increase in the most recent decade, conclusions of recent, shorter-term studies (e.g., 20 years of data) might have been different. For example, if the spruce budworm outbreak had been in the 1980s instead of the early 1970s, patterns of increase in many species might have generated less concern for conservation. Because of the long duration of our data set, we have been able to place these short-term, but statistically significant changes, in perspective. Any future patterns of increase shown by some

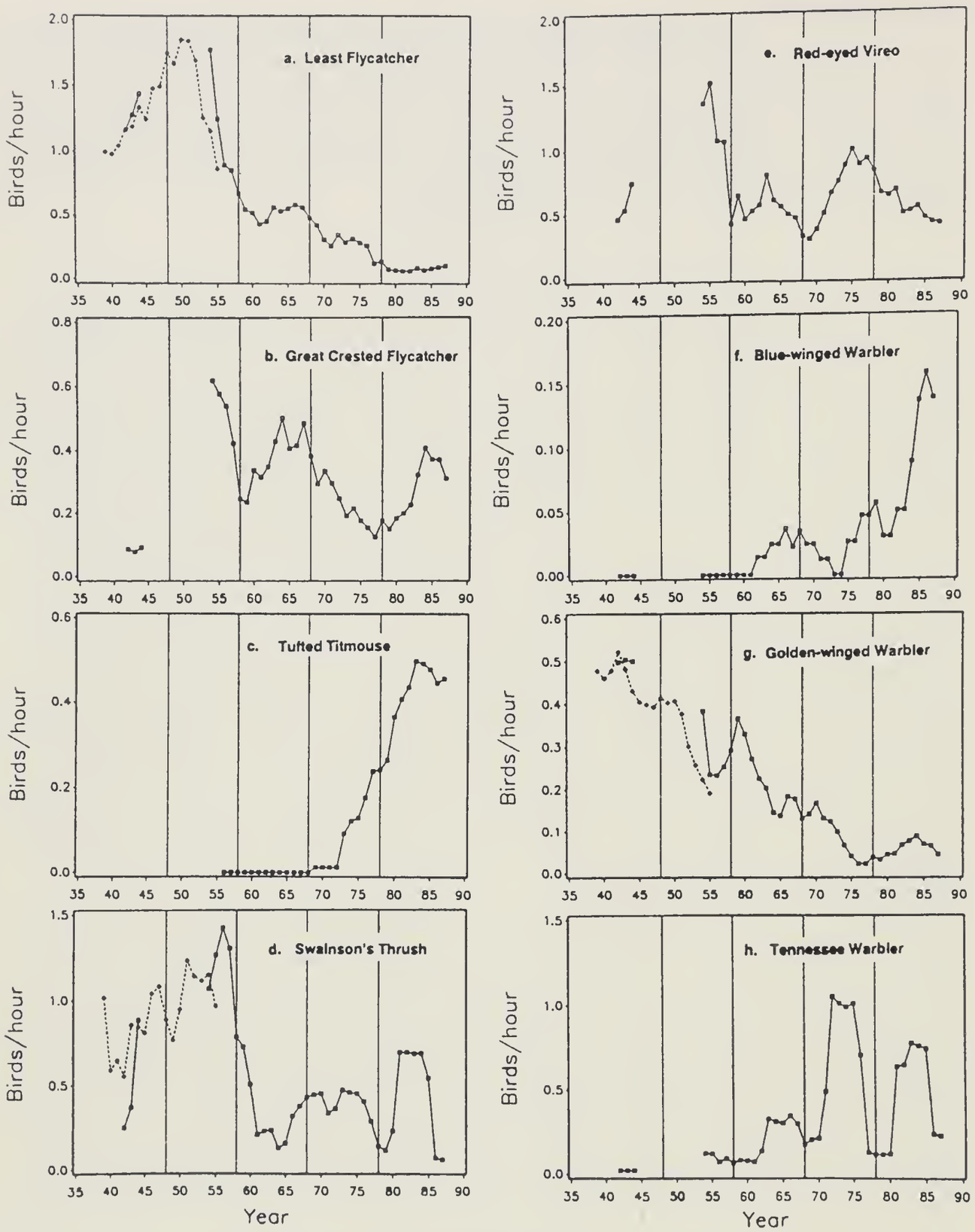

FIG. 1. Plots of population trends of 26 Neotropical migrant species and two temperate, resident species. Solid lines connecting squares represent data points derived from census data collected by N. P. Hill, and dashed lines connecting diamonds represent data points derived from L. Griscom data. Each point represents the moving average for five equally weighted years of data.

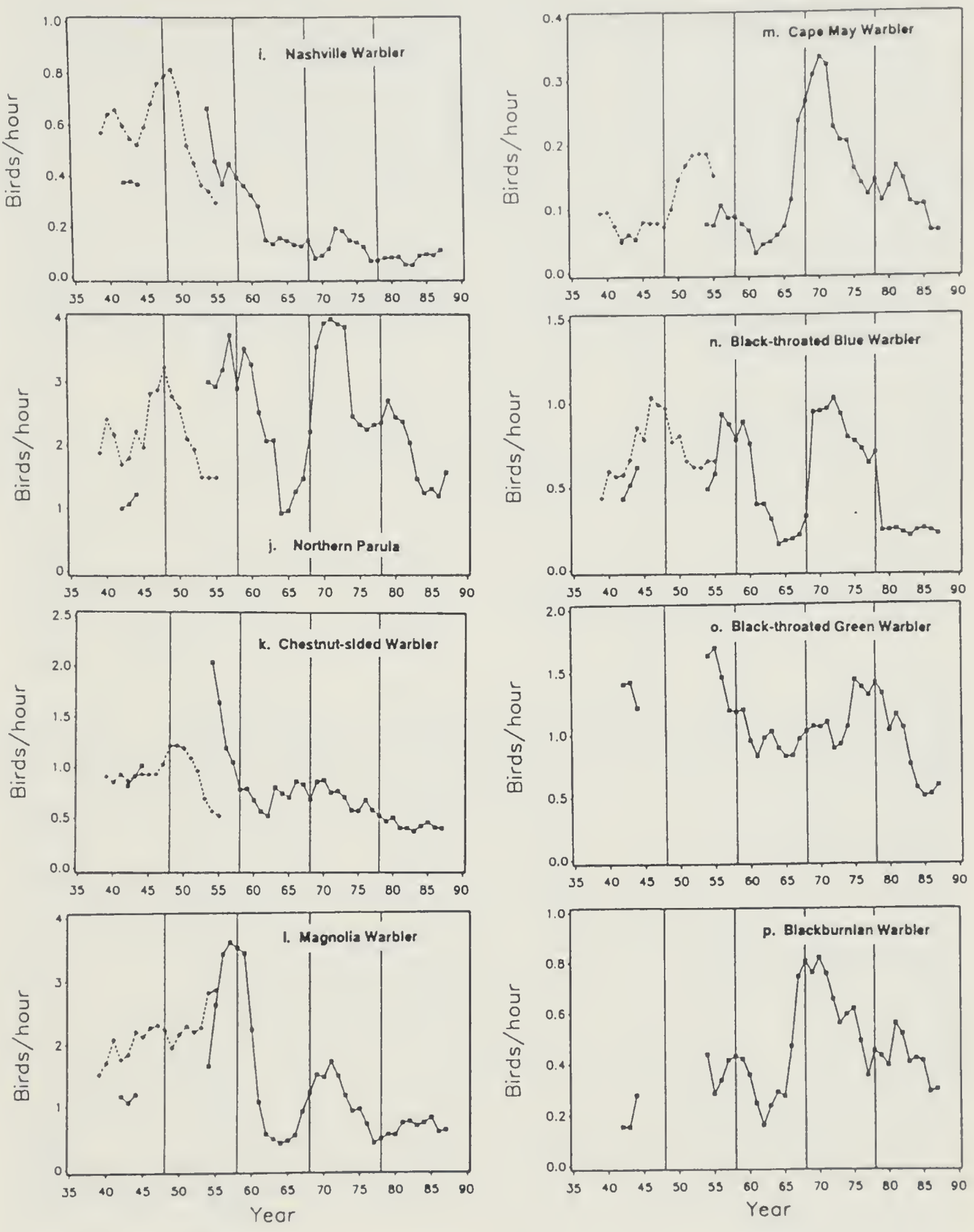

FIG. 1. Continued.

species will not warrant dismissal of conservation concerns. Rather, it should be recognized that some populations will naturally cycle; our concern is that the fundamental long-term population trend is negative and significant for most species.

Why some species showed a switch in trend direction or significance

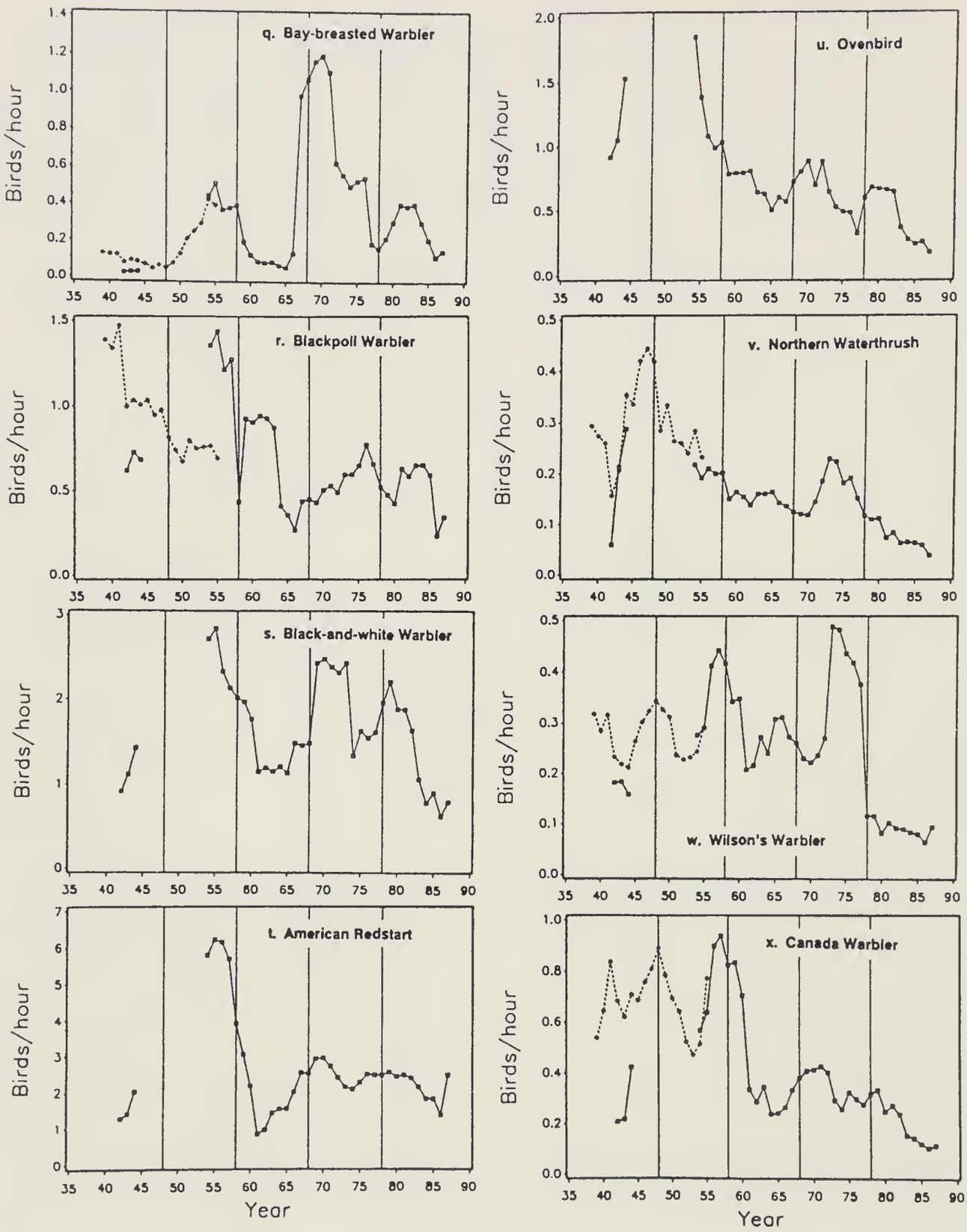

FIG. 1. Continued.

and others showed steady, monotonic declines is not known. The Least Flycatcher, which showed a consistent decline since about 1950 in our data set, also showed a consistent decline at the Hubbard Brook Experimental Forest in New Hampshire since 1969, when censuses began there (Holmes and Sherry 1988). Holmes et al. (1986) attributed this pattern

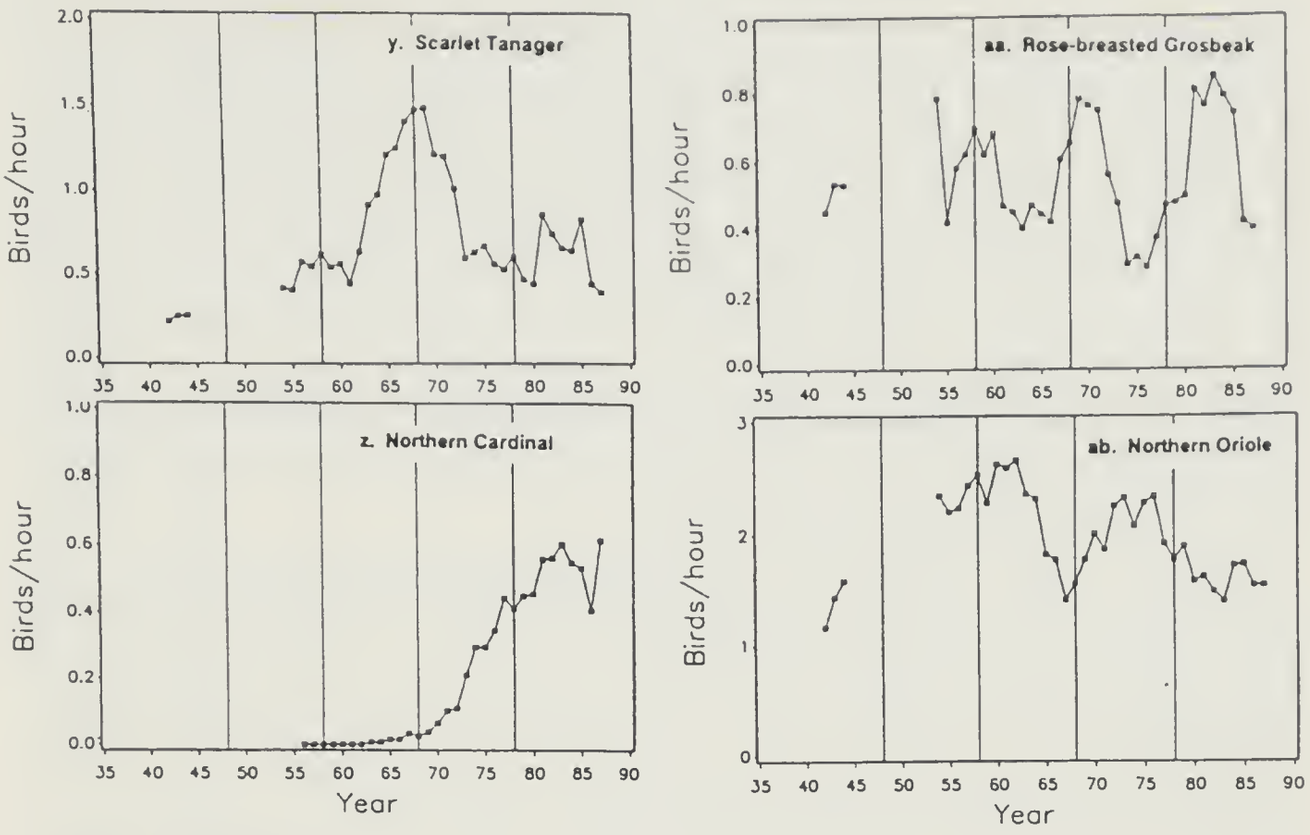

FIG. 1. Continued.

of decline to gradual loss of intermediate stages of forest succession in the region, which are preferred by Least Flycatchers. We found other species that showed a similar pattern of decline (e.g., Nashville Warbler, Chestnut-sided Warbler, Magnolia Warbler, Canada Warbler, Wilson's Warbler), and which also commonly breed in second-growth habitats. Two other species that demonstrated such declines, however, are not associated with such breeding habitats (Ovenbird, Northern Waterthrush). The Golden-winged Warbler decline probably can be attributed to the range expansion of the Blue-winged Warbler (Confer and Knapp 1979), although competitive interactions are only speculative.

Three species are known to be responsive to outbreaks of the spruce budworm (Tennessee Warbler, Cape May Warbler, Bay-breasted Warbler) (Morse 1978, Harrison 1984). All of these species showed cyclical patterns, and strong peaks in abundance in the early 1970s that coincided with a known budworm outbreak. We do not know if other peaks in these species' trends (see Figs. 1h, m, q) can be attributed to insect outbreaks. Several other warbler species also showed peaks in abundance in the early 1970s that might have been a response to the spruce budworm outbreak across southeastern Canada and the northeastern United States, even though they are not known to be "budworm" species.

The nature of our data set presents some limitations in interpretation. The data were not collected using a standard, recognized sampling pro-

tocol, and the amount of sampling varied from year to year. Furthermore, weather can cause considerable annual variation in the observed numbers of migrating birds, yet migration capture data collected at bird observatories has proven useful in documenting population trends (Hussell 1981, Hagan et al., in press, Hussell et al., in press). These factors imposed variation in our data that might not have occurred otherwise. However, the same sampling sites were visited annually, data were recorded carefully, and abundance indices were converted to birds per hour of effort. Given the unusual temporal extent of the data set, we believe the data set surmounted these potential limitations because some trends could be corroborated using other data sources.

Observer bias could be an inherent complication in this study. For example, observers changed in the mid-1950s (for 14 species). However, inspection of some of the trends of these species shows general agreement during the observer transition (see Fig. 1a, d, g, i, l, m, n, q, v, w and x). Having only two observers over a 53-year period could also be viewed as a benefit, because annual variation in counts has not been due to differences in observer skill. Moreover, both observers were highly skilled from the start of sampling. Griscom's health was failing in the late 1950s and could partially explain the discrepancies. Also, because the two observers were sampling on different days during the period of overlap, perfect agreement cannot be expected. Hill's hearing was tested by audiometry in 1991 and found to be normal. Thus, it is unlikely that hearing loss has affected our results. Moreover, many declines have been apparent for 20 or more years, and most birds were detected during migration censuses by sight and not sound.

If our data represent real population changes, rates of decline are distressing. Of the 26 Neotropical migrant species we studied, 18 have declined significantly over the past 40 to 50 years. For most species, the decline has not been limited to the past 20 years, and the long-term rate of change for all 26 Neotropical migrants averaged −0.94% per year. This rate of decline would put the "average" species now at 62% of population levels of 50 years ago (Fig. 2). An annual rate of decline of −2% per year and −3% per year, which some species showed, would put their populations at 37% and 21%, respectively, of levels of 50 years ago (Fig. 2). Ignoring species divisions, and using the 38 years of Hill data alone (34 smoothed points, 1954–1987), the number of Neotropical migrants seen per hour of effort in 1987 was only 36% of the 1954 value (Fig. 2). This rate of decline was more extreme than the average rate because the distribution of rates was not normal. That is, more abundant species declined at disproportionately higher rates.

As with any migration count index of population change, it is difficult

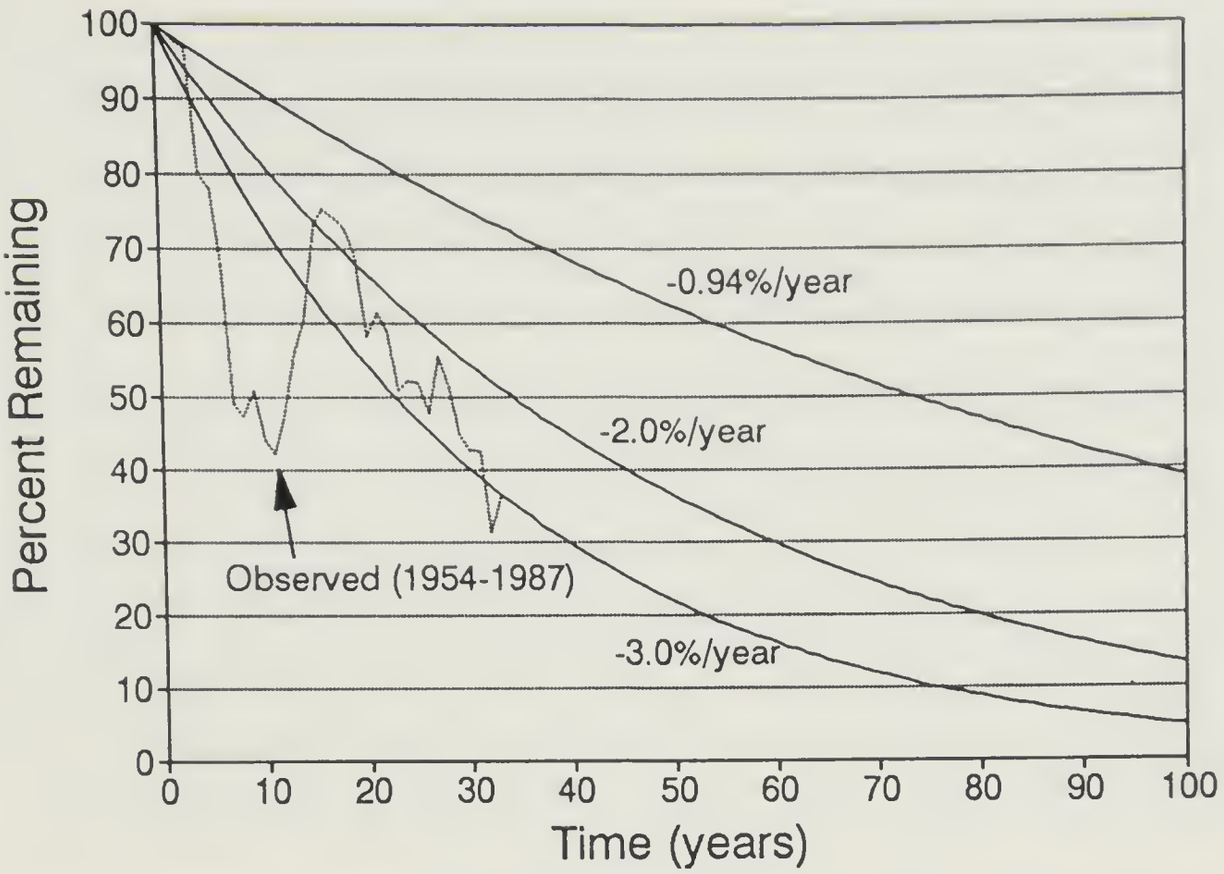

FIG. 2. Percent of populations remaining over time based on: (1) the annual mean rate of change for 26 Neotropical species (−0.94%), (2) a hypothetical 2% and 3% rate of decline, and (3) actual observed numbers of Neotropical migrants per hour of effort, ignoring species, using only the Hill data (smoothed data, 1954–1987).

to define the scope of inference (Atwood, in press, Hagan et al., in press). Origins and destinations of migrant birds sampled in this study were not known, but breeding destinations were almost certainly north of the censused areas. For this reason, the sample of migrants in this study represents populations of regional extent. Scale is an important consideration in interpretation of trend data, because species' trends can differ in slope and significance, depending on the region of study (Sauer and Droege 1990, James et al., in press, Sauer and Droege, in press). Thus, our conclusions should not be interpreted as representing the range-wide changes in species.

Observed results in this or any population monitoring study might be caused by habitat changes along migration routes, changes in breeding habitat, changes in wintering habitat, or any combination thereof. However, for some species in the northeast, such as the Blue-winged and Golden-winged warblers, and the Least Flycatcher, the primary force driving the population changes have most likely been a result of breeding ground events. The Blue-winged Warbler was described by Robbins et al. (1989) as a forest-wintering species that was decreasing on a continental

scale. If tropical deforestation were the sole factor controlling its populations over its entire range, we would have expected to see a population decline as well, rather than the increase that we observed. Conversely, the Least Flycatcher, a scrub-wintering species, showed one of the most dramatic declines in our data set. These results illustrate the need for caution in assigning cause to observation. Although we believe tropical deforestation is a serious long-term threat to Neotropical migrant landbirds, patterns of population change must be examined at the species level when analyzing a geographically restricted data set such as ours. Although much discussion has centered on the causes of recently observed population changes (Hutto 1988, Morton and Greenberg 1989, Askins et al. 1990), it would be unwarranted for us to attribute a general cause for long-term population declines based on our data. Whatever the cause(s) of these changes, this data set shows many significant, very long-term declines in abundance in the Northeast, corroborating other such reports, and indicating that much more work is needed on the relationship between habitat change in the Nearctic and Neotropics, and bird populations.

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DIURNAL ACTIVITY BUDGET OF FEMALE RUDDY DUCKS BREEDING IN MANITOBA

MICHAEL W. TOME[1]

ABSTRACT.—I observed activities of pre-laying, laying, and incubating female Ruddy Ducks (*Oxyura jamaicensis*). Foraging comprised 66.3% and 54.4% of diurnal activities during pre-laying and laying, respectively. Time spent resting increased from 11.0% during prelaying to 73.5% during incubation, primarily because of time spent on the nest. Female Ruddy Ducks took 7.4 ± 3.2 incubation recesses during a 24-h period and recesses averaged 39 ± 4 min (mean ± SD). Foraging comprised 76.4% of recesses and accounted for 185.0 min of foraging/day. Female Ruddy Ducks meet most of their energy needs exogenously. Their pattern of energy acquisition for and allocation to reproduction supports the general hypothesis that smaller-bodied waterfowl can store less nutrient reserve than large-bodied waterfowl and must rely more on exogenous energy during reproduction. *Received 15 June 1990, accepted 3 Nov. 1990.*

Comparative studies of waterfowl behavior and energetics during reproduction indicate that females of different waterfowl species have evolved various patterns of energy/nutrient acquisition and allocation which decrease daily dietary requirements for reproduction during peak periods of energy/nutrient demand (Ricklefs 1974). To meet energy/nutrient demands of egg laying and incubation, some species store lipid and/or protein before arrival on breeding areas (Korschgen 1977, Ankney and MacInnes 1978, Raveling 1979, Krapu 1981), whereas others acquire energy/nutrients after arrival on breeding areas (Drobney 1980, 1982; Tome 1984; Brown and Fredrickson 1987a; Ankney and Afton 1988; Hohman 1986) and catabolize these reserves during laying and incubating. Female waterfowl adjust their activities during reproduction to meet changes in energy demands (Afton 1979, Gray 1980, Hohman 1986, Brown and Fredrickson 1987b).

Female Ruddy Ducks (*Oxyura jamaicensis*) produce eggs that are among the largest proportional to body size of all waterfowl (Lack 1968). Nonetheless, they meet most of their energy needs through dietary intake on the breeding grounds (Tome 1984). In this paper, I describe diurnal activity budgets of female Ruddy Ducks during pre-laying, laying, and incubating and discuss how their behavior relates to their energy/nutrient acquisition for and allocation to reproduction.

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STUDY AREA AND METHODS

I derived activity-budgets of female Ruddy Ducks breeding in the prairie-pothole region of southwestern Manitoba, approximately 16 km southeast of Minnedosa, during the spring and summers of 1979–1980. Topography in this region is a knob and kettle land-type interspersed with numerous wetlands ranging in size from permanent (>4 ha) ponds to small (<10 m^2) seasonal sloughs. This area was described in detail by Evans et al. (1952).

I used focal animal observations (Altmann 1974) to sample activities of female Ruddy Ducks during pre-laying, laying, and incubating. All birds observed (N = 12) were individually marked with imped (Wright 1939) colored tail feathers or were recognized by unique plumage characteristics. An electronic metronome (Wiens et al. 1970) was used to delineate sampling points at 15-sec intervals. I also measured the duration of the first dive and dive-pause during feeding bouts. I recorded the behavior of a bird chosen at random from among those available for observation during 2-h periods that I systematically scheduled three times each day. All daylight hours were sampled every five days. I determined each bird's reproductive status by locating its nest, determining the stage of incubation, and back-dating to each observation date.

I categorized behaviors of female Ruddy Ducks as (1) rest (sleep, loaf, incubate), (2) comfort (preen, wing stretch, etc.), (3) alert, (4) swim, (5) bathe, (6) dive, (7) dive-pause (time spent between dives), and (8) social (courtship displays, chases, agonistic behavior, etc.). A small (4–6 g) transmitter was attached to the central three rectrices of three birds. I monitored signal attenuation when birds dived and thus recorded nocturnal feeding. The transmitters fell off after 3–5 days, so I collected only limited nocturnal data.

I observed the behavior of three females on the nest during incubation and during recesses; I derived diurnal activity budgets during incubation from these females. I observed six other incubating females during recesses only. I used the observations of these and the previous three females to determine behavior during recesses. I measured nest attentiveness (amount of time spent incubating) and number, duration, and time of incubation recess (definitions after Afton 1980) of five females with a nest monitor that recorded presence or absence of the female on the nest (Cooper and Afton 1981). I obtained a complete 24 day record for one female; the other nests were monitored for 20, 17, 12, and 11 days, respectively. Incomplete records resulted because nests were depredated or found several days into incubation.

Percentage of time engaged in each activity was calculated by dividing the number of times an activity was observed by the total number of observations in an observation session. Only observation sessions of at least one h were included in the analysis except for the analysis of recesses which, because they were <one h, were all included in this calculation.

Differences in percent time engaged in each activity among pre-laying, laying, and incubating were detected with Kruskal-Wallis tests (Conover 1980). Behavior during recesses was not included in the analysis. If differences among behaviors were detected, the nonparametric analog to the Least-Significant Difference multiple comparison test was employed to determine where differences occurred (Conover 1980). Differences were considered significant at $P \leq 0.05$.

RESULTS

Percent time engaged in various activities differed among reproductive periods (Table 1). Dive and dive-pause (foraging) activities were dominant during pre-laying and laying. Time spent diving was greater during pre-laying than during laying ($P \leq 0.05$); however, the dive-pause activity

TABLE 1
DIURNAL TIME-ACTIVITY BUDGET (PERCENT TIME ± SD) FOR BREEDING FEMALE RUDDY DUCKS

Behavior	Pre-laying N = 41 h	Laying N = 15 h	Incubating	
			N = 22 h	N = 42 recesses
Rest	11.0 ± 2.4 A[a]	23.4 ± 6.0 B	73.5 ± 7.1 C	2.2 ± 0.1
Preen	9.3 ± 1.4 A	9.2 ± 2.2 A	10.7 ± 2.5 A	9.9 ± 0.2
Alert	1.4 ± 0.3 B	tr A	tr A	0.4 ± 0.01
Swim	10.0 ± 1.5 B	9.6 ± 1.7 B	0.6 ± 0.2 A	3.6 ± 0.1
Bath	1.0 ± 0.1 A	1.1 ± 0.3 A	1.1 ± 0.6 A	6.3 ± 0.4
Dive	44.1 ± 2.6 C	32.5 ± 6.0 B	8.4 ± 0.8 A	46.7 ± 0.3
Dive Pause	22.2 ± 1.4 B	21.9 ± 3.1 B	5.4 ± 0.1 A	29.7 ± 0.2
Social	1.0 ± 0.1 B	2.3 ± 0.9 B	0.3 ± 0.01 A	1.2 ± 0.01

[a] Within a row, means with different letters are significantly different ($P \leq 0.05$).

did not differ between these periods. Dive and dive-pause duration averaged 21.7 ± 2.9 sec and 9.7 ± 5.8 sec (mean ± SD; N = 140), respectively, and did not differ among reproductive periods (ANOVA; $P > 0.05$). Percent time engaged in preen, alert, swim, bathe, and display activities was not different ($P > 0.05$) between pre-laying and laying. Frequencies of all behaviors, except rest, maintenance activities (i.e., bathe or preen), and alert were reduced ($P \leq 0.05$) during incubation because most behavior on the nest was either rest, preen, or alert.

Incubation recesses were taken at all times of the day and night (see fig. 5 in Cooper and Afton 1981). Incubation constancy (percent of time spent on the nest), calculated from nest monitors, was 83.1 ± 2.9% (N = 5 females; mean ± SE). Female Ruddy Ducks left the nest 7.4 ± 3.2 times per day, and each recess averaged 39 ± 4 min (mean ± SD). Most of the recess was spent foraging (dive and dive-pause activities combined) (Table 1).

Radiotelemetry showed that pre-laying female Ruddy Ducks fed at night. I was unable to radio-mark laying or incubating females, however, incubating females likely fed during night-time recesses.

DISCUSSION

Activity budgets of female Ruddy Ducks, particularly foraging behavior, reflect their need to acquire nutrients and energy on the breeding grounds for egg production and incubation. Pre-laying and laying females spent most daylight hours foraging, and limited data indicate that they also fed at night. Incubating Ruddy Ducks foraged for most of their recesses.

TABLE 2
INCUBATION RECESSES AND LENGTH OF FEEDING PERIOD FOR EIGHT ANATIDS

Species	Incubation period (days)	Average weight (g)[i]	Time off nest/day (min)	Mean proportion of time spent feeding	Feeding time/day (min)
Branta canadensis[a]	27	5034	20.2	0.38	7.6
Melanitta fusca[b]	25	1200	223.0	0.61	136.0
Anas platyrhynchos[c]	26	1100	78.0	0.67	52.6
A. rubripes[b]	26	1100	189.6	0.70	132.7
A. clypeata[e]	23	635	221.3	0.68	151.1
Oxyura jamaicensis[f]	24	511	243.4	0.76	185.0
A. discors[g]	23	376	289.0	0.60	173.4
A. crecca[h]	24	343	296.6	0.65	193.4

References: [a] Cooper (1978); [b] Brown and Fredrickson (1987b); [c] Caldwell and Cornwell (1975); [d] Ringelman and Owen (1980); [e] Afton (1979); [f] this study; [g] Miller (1976); [h] Afton (1978); [i] Palmer 1976.

Female Ruddy ducks do not accumulate large lipid or protein stores before laying to defray costs of egg production and incubation, as do many large-bodied anatids, for example, Mallards (*Anas platyrhynchos*) (Krapu 1981) and Lesser Snow Geese (*Chen c. caerulescens*) (Ankney and MacInnes 1978). Female Ruddy Ducks catabolize approximately 31 g of lipid during laying, which provides 35% of the lipids for clutch formation; the remainder of the lipid and all protein requirements of clutch formation are met exogenously (Tome 1984).

Afton (1980) hypothesized that smaller bodied waterfowl are not able to store large (relative to large-bodied waterfowl) lipid reserves and, thus, are more dependent upon exogenous energy during incubation. The activity budgets (this study) and pattern of endogenous/exogenous energy allocation for reproduction of the female Ruddy Duck (Tome 1984) support this hypothesis. During incubation, female Ruddy Ducks catabolize approximately 36 g of lipid, which provides about 21% of their basal metabolic energy (Tome 1984). Thus, they must take incubation recesses to obtain the remaining 79%.

In comparison with other North American waterfowl, incubating female Ruddy Ducks spent proportionately more time feeding during recesses (Table 2). Except for Green-winged Teal (*Anas crecca*) (Afton 1978), incubating Ruddy Ducks spend more time/day feeding than do other species of waterfowl examined thus far, again supporting Afton's (1980) body size/nutrient reserve hypothesis.

The pattern of incubation recesses exhibited by female Ruddy Ducks is unusual relative to that of other waterfowl studied. Female waterfowl typically take one to three incubation recesses of 1 to 2 h each per day.

Ruddy Ducks take shorter recesses (averaging 39 min) and take them at all times of night and day, as also reported by Siegfried et al. (1976) (N = 2 females). This appears typical of Oxyurini, as female Maccoa Ducks (*Oxyura maccoa*) and White-headed Ducks (*O. leucocephala*) take frequent, short, incubation recesses (Siegfried et al. 1976, Matthews and Evans 1974).

Siegfried et al. (1976) suggested that length of Ruddy Ducks' recesses was a trade-off between cooling and re-warming rates of eggs (e.g., Drent [1975] found that rewarming eggs takes longer than it does for them to cool) and time necessary for a female to fill her esophagus with food. However, length and timing of recesses is likely related to some factor other than the time necessary to fill the esophagus. Breeding Ruddy Ducks feed primarily on chironomid larvae (Siegfried 1973, Tome 1981, Woodin and Swanson 1989), and these invertebrates pass very quickly from esophagus to gizzard (Swanson and Bartonek 1970). Only rarely were Ruddy Ducks' esophagi filled with larvae, even though birds were often observed for >20 min before they were collected (Tome, unpubl. data).

Female Ruddy Ducks typically feed on the pothole where their nest is located (Tome 1984). The high levels of feeding observed in this study and the energy/nutrient demands that female Ruddy Ducks meet with dietary intake (Tome 1984) highlight the importance of wetland selection for adequate food resources by breeding female Ruddy Ducks.

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POLYTERRITORIAL POLYGYNY IN THE AMERICAN REDSTART

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ABSTRACT.—The first six cases of bona fide polygyny are described in American Redstarts (*Setophaga ruticilla*), along with associated male song behavior, nesting and parental care, and a case of female-female aggression. Typically, older (than yearling) males sought secondary reproductive opportunities by traveling 100–400 m through continuous forest to advertise new territories using "repeat-mode" song, typical of genuinely unmated males; and fed primary nestlings and fledglings more than secondary ones. Estimated frequencies of polygynous mating were 15.8%, 5.3%, and 8.0%, respectively, in 1988, 1989, and 1990 (N = 63 color-banded males under close observation), but additional cases of polyterritorial advertisement behavior were noted. Polygyny appears to be a facultative strategy by which males obtain extra reproductive opportunities deceptively, on secondary territories far removed from sites of primary territories and nests. However, we have not ruled out the possibility that secondary females could compensate for reduced parental care by mating with higher quality mates or on better territories than otherwise available. Polygyny may have been facilitated in our study population by a relatively low abundance of males and an unusual abundance of yearlings. *Received 30 April 1990, accepted 6 Feb. 1991.*

Polygyny is widespread in passerine birds, even in predominantly monogamous species (Ford 1983). The evidence for polygyny in primarily monogamous species is often anecdotal, however, and even in well studied species often provides insufficient behavioral or ecological context with which to evaluate which of various forms polygyny has taken (Searcy and Yasukawa 1989). We document here the first bona fide cases of polygyny in the American Redstart (*Setophaga ruticilla*), and provide preliminary information with which to assess the form polygyny takes in this species. We describe associated territorial and song-advertisement behavior, nesting chronology, parental care, a case of female-female aggression, and a number of additional cases of males attempting to attract multiple mates. We then discuss the form polygyny takes in redstarts and the ecological circumstances favoring it in this species. Previous reports of polygamy in redstarts, describing cases of two unbanded females at one nest (Barney 1929, Hodges 1948), are insubstantial, because they provide no information on the reproductive contributions of these two females, and fail to rule out the possibility that one of these "females" was actually a yearling male, which can closely resemble a female (Rohwer et al. 1983).

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STUDY AREA AND METHODS

Our study took place in a nearly mature and continuous northern hardwoods forest in the Hubbard Brook Experimental Forest (USDA, Forest Service Experiment Station) in West Thornton, New Hampshire. Locations of American Redstarts, their nests, and behaviors were studied in a 180-ha area, but concerted effort to color mark all individuals and find their nests was restricted to a 34-ha area, gridded at 50-m intervals. The study areas and avifauna have been described by Sherry and Holmes (1985) and Holmes et al. (1986). Most males and several females involved in these observations were identified by unique combinations of colored and aluminum leg bands, or by peculiarities or unique patterns of song types. This allowed detection and monitoring of their movements in heavily forested habitat. Nests were observed, usually without using a blind, from a minimum distance of 20 m. Numbers of trips made to the nest by both the male and female at each nest were recorded, usually in one-hour watch periods spread throughout the day. Song behavior terminology follows MacNally and Lemon (1985): "Repeat-mode" uses only one song type, usually the "accented-ending" song (Ficken 1962), whereas "serial-mode" involves series of alternating song types, usually exclusive of the repeat-mode type. Genuinely unmated male American Redstarts, prior to the arrival of females, characteristically broadcast continuous, relatively loud, high rate, repeat-mode songs (Ficken 1962, Ficken and Ficken 1970). Upon mating, the rate of repeat mode song slows, and the serial mode begins to occur more frequently as nest building progresses. Those males remaining unmated after arrival of females rarely, if ever, sing in serial mode. We refer to bouts of continuous, relatively loud, repeat-mode song behavior as "advertising," regardless of when in the season they occurred, and regardless of whether a bird was known to be mated.

RESULTS

Frequency of polygyny and territorial advertisement.—We confirmed two cases of polygyny in each of 1988 and 1990, and found two other likely cases in 1988 and one in 1989. These numbers represent 15.8% (N = 19; only three of the four 1988 cases were on the 34-ha area), 5.3% (N = 19), and 8.0% (N = 25) of all males in 1988, 1989, and 1990, respectively, on the 34-ha study area. We based these estimates of polygyny frequencies on our 34-ha study area, in which we were most likely to detect polygyny because of the color-banded males and intensive nest searches there. We first describe two 1988 cases in greatest detail, then describe briefly additional cases of polygyny and polyterritorial advertisement.

The two cases confirmed in 1988 involved a bigamous male (henceforth M1) and a trigamous male (M2), which were three and ≥ 4 years old, respectively, based on when they were banded. M1's primary female was banded the previous summer, and so was ≥ 2 years old. Two of the other four females mated to M1 and M2 were banded late in the 1988 season: The secondary mate of M1 was a yearling female, and the tertiary mate of M2 was probably a yearling as well, based on rectrix characteristics (Pyle et al. 1987).

Both M1 and M2 resumed advertising song behavior in at least two

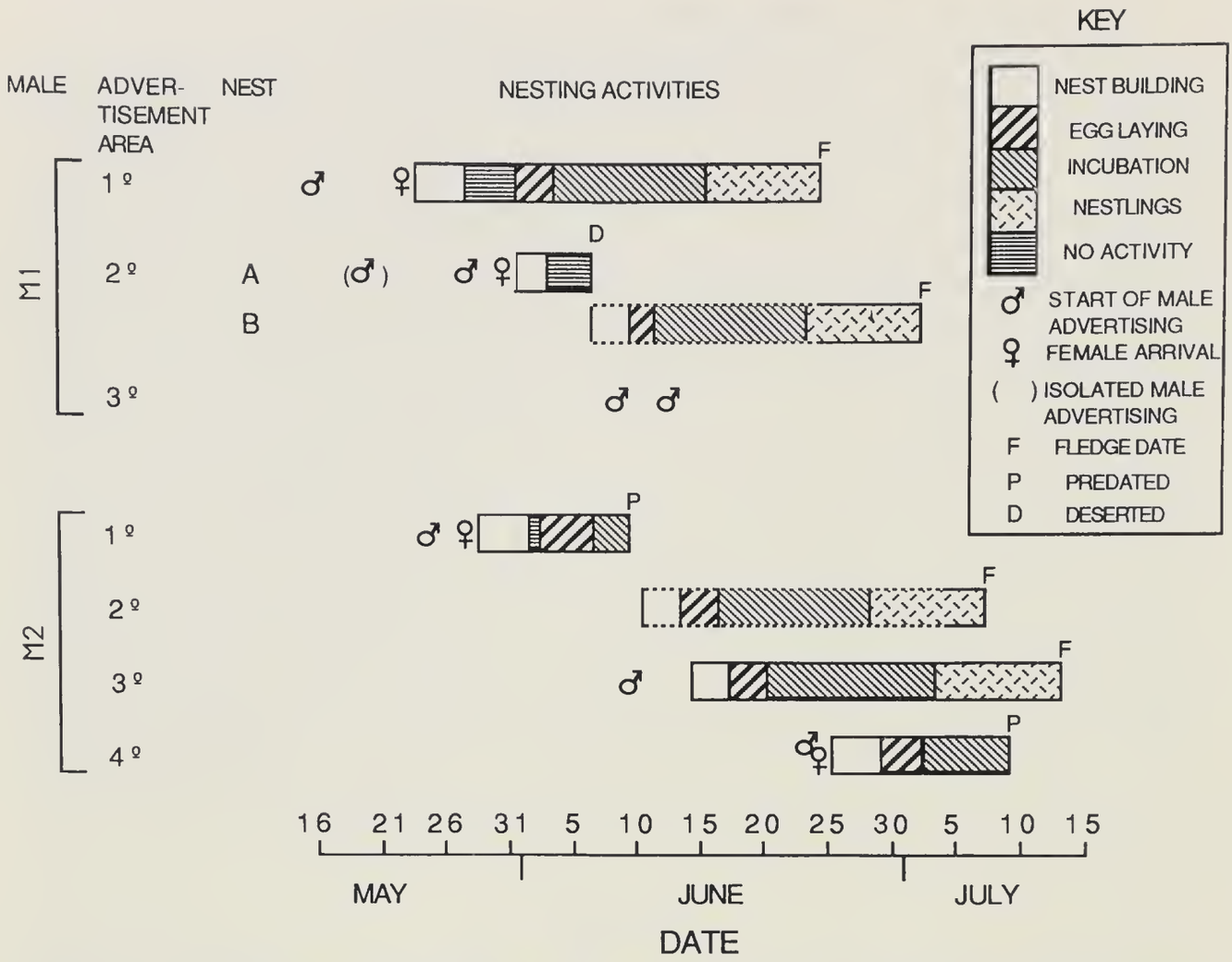

FIG. 1. Chronologies of breeding season activities for two polygynous male American Redstarts observed in 1988, Hubbard Brook Experimental Forest, New Hampshire. M1 and M2 designate male one and male two, respectively, and their home ranges are numbered chronologically, beginning with the first territory advertised. Dashed horizontal lines designate inferred dates of activities, based on typical redstart periods for the different nesting stages. Parentheses surrounding the first date that male M1 advertised at his 2º area indicate one isolated day in which this male sang at the site, but did not persist there until the female was observed on 31 May.

separate areas after mating with a female at another initial location. Both males resumed advertising on secondary and tertiary advertising areas no later than the late building phase of their previous nest (Fig. 1). The exception to this was M1's secondary advertising area, where we once observed him singing subsequent to establishment of his first advertising area, but before his first female was known to have arrived (Fig. 1). However, he was not observed in the second area again until the late building phase of his first nest.

Advertising areas were locations of repeat-mode singing prior to mating and nest building (Fig. 2). We hesitate to refer to these areas as territories, since no other males established themselves within the continuously suit-

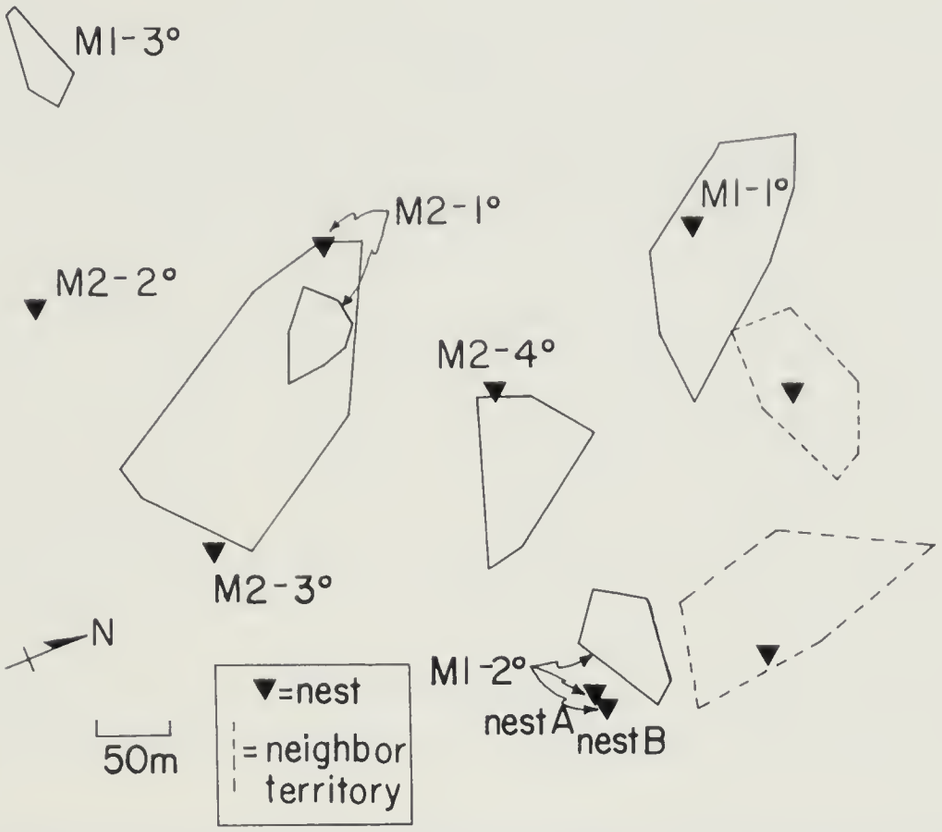

FIG. 2. Map showing locations of multiple advertising areas within home ranges of two polygynous male American Redstarts observed in 1988, Hubbard Brook Experimental Forest, New Hampshire. Nest locations are shown by triangle, and territories of two other neighboring males are shown with dashed lines. Arrows emanating from M1–2° and M2–1° indicate particular advertising territory and associated nest(s). See legend to Fig. 1 and text for descriptions of other symbols.

able habitat between the advertising areas of either M1 or M2, such that both of these males had relatively wide corridors in which to travel between their different display areas and nests (Fig. 2). One can argue that the area inclusive of all nests and advertising areas for either of these males was that male's territory (e.g., DellaSala 1986), even though these latter areas were larger than the territories of other males. However, these males did not sing throughout their home ranges, but instead concentrated advertising behavior in the smaller areas indicated (Fig. 2). M1 attracted a mate in two of his three advertising areas. His primary display area was less than 100 m from where he had been banded as a yearling in 1986; and his tertiary advertising area, to which he never successfully attracted a mate in 1988, was the area in which he had successfully mated and in which young were fledged in both 1986 and 1987. M2 succeeded in mating at all three of the areas where we observed him advertising. We did not observe M2 advertising in the vicinity of his secondary nest because this nest was not found until three days before its chicks fledged (Fig. 1). All females of both these males nested within or immediately adjacent to the

display areas of their respective mates (Fig. 2). If we define distances between advertising areas as the distance from a male's previously established nest to the nearest location where he subsequently resumed advertising that same breeding season, then distances between M1's advertising areas were 245–450 m, and those for M2 ranged from 120–180 m.

Nesting chronology.—Three nests were built on display areas where only male M1 sang or was otherwise observed repeatedly. M1's primary nest, and the second nesting attempt (B) on his secondary display area successfully fledged young (Fig. 1). The first nesting effort on his secondary display area (A) failed before we had ascertained whether laying had begun. Eighteen days after activity at this nest ceased we observed M1 feeding nestlings at the B nest, 10 m distant from the A nest (Fig. 2). Because these nests were so close together, were constructed in such similar sites, and building of nest B was inferred to have begun by 6 June (see below for modal chronologies at typical redstart nests), the day after the first nest was probably destroyed (Fig. 1), we believe that the two nests were built by the same female.

Four chicks fledged from M1's first nest on 24 June. During the period when he was feeding fledglings from this primary nest, he also fed nestlings in his secondary nest B. We simultaneously monitored recent fledglings from M1's primary nest and nestlings in his secondary nest (B) on nestling period days 5–7 (where day 0 was the first day in which any nestlings had hatched—see Fig. 1). Only 9% of the sightings of M1 bringing food to chicks were in the vicinity of secondary nest B (N = 391 min). His secondary nest B fledged at least three chicks on 1–2 July.

Four nests were built in association with the display areas of male M2 (Fig. 1), and young fledged from his secondary and tertiary nests. Because his secondary nest was discovered when it contained nestlings, the transition dates for phases in the nest cycle were extrapolated backwards from the fledge date (Fig. 1). Modal nest phase lengths were used in these extrapolations (Sherry, unpubl. data): Nest-building = 4 days, egg laying = 4 days (or one day per egg in clutches with fewer or more eggs than four), incubation = 11 days, nestling-feeding = 9 days. M2's first nest became inactive during incubation. We do not know whether or not his secondary nest was built by his mate from his primary nest, but the female at the secondary nest could have been the same individual as the one which abandoned the primary nest, since M2's secondary mate had sufficient time (assuming modal durations of nesting stages described above) to accomplish all nesting tasks by July 7 if she had begun building on 10 June, the day after M1's primary nest was depredated (Fig. 1). M2's first successful nest, on his secondary display area (Fig. 2), fledged four young on July 7. M2 fed fledglings from this first brood while feeding the nestlings

TABLE 1

COMPARISON OF NESTLING-FEEDING BEHAVIOR OF TWO POLYGYNOUS AND FIVE MONOGAMOUS AMERICAN REDSTART MALES IN THE HUBBARD BROOK EXPERIMENTAL FOREST, NEW HAMPSHIRE, 1988

Male	Nest	Nestling days[a]	Percent feeding trips by male (per nest)	Observation time (min)
M1	1°	2	85–100	57
	2°	1–7	4–10	617
M2	2°	7–8	59–72	291
	3°	3–10	34–50	720
Monogamous males		5–7	61–67	1440

[a] Days since at least one nestling hatched (=day zero).

of his second (tertiary nest, Fig. 1). During simultaneous surveillance of these fledglings and M2's tertiary chicks on their nestling period days 4–6 (nestling day 4 for tertiary chicks corresponded with the fledge day at his nest on his secondary display area—Fig. 1), only 33% of his sightings were near his tertiary nest (N = 291 min). His tertiary nest fledged four young on 13 July. His quaternary nest was active during this period, but it was not observed concurrently to see if he visited the site. However, earlier, during the period that his tertiary female was incubating and his quaternary female laying, he was never sighted at either of their nests during simultaneous watches (150 min). He may have been attending nestlings at his secondary nest, which we had not yet discovered, during these 150 min of observation. M2's quaternary nest was deserted about half way through the incubation phase.

Parental care.—Both males contributed more to feeding dependent young at their earlier than their later nests, as quantified by percentage of trips made by the male (Table 1). M1 made 85–100% of the feeding trips at his primary nest, but this is based on a short observation period when cool weather may have increased his relative contribution to feeding nestlings (K. E. Omland and T. W. Sherry, unpubl. data). We do not know how many trips he contributed to this nest late in the nestling stage, but judging by his contribution to fledglings (see below) it was almost certainly more than the 4–10% he contributed to his secondary nest. M2 contributed more trips at his earlier (secondary) nest (59–72%) than at his later (tertiary) nest (34–50%—Table 1). The second trend to note is that both polygynous males contributed proportionately fewer feeding trips to nestlings at their secondary nests than five monogamous two-year-or-older males also observed in 1988, each of which contributed 61–67% of feeding trips (Table 1). Thus the females at M1's secondary nest and at M2's

tertiary nest fledged young with reduced feeding assistance from their mates. Three widowed redstart females and an older male without a mate during at least the final two days of the nestling period have all fledged young successfully (Sherry, unpubl. data). These observations indicate that redstarts can fledge young with reduced parental effort from a mate, unlike Black-throated Blue Warblers (Petit et al. 1988), although redstart nestlings starve in some years even with both parents attending nests (Sherry and Holmes, in press).

For most broods (M1's primary, and M2's secondary and tertiary ones) each parent fed half the brood exclusively, a brood division described previously in redstarts by Boxall (1983). We lost track of all females with broods on the second day after fledging.

The location of M1's primary nest fledglings shifted toward his secondary nest over several days. He spent most of his time singing serial mode songs, alternating with feeding his two fledglings. Periodically he moved away from these fledglings, switched to repeat mode song and made one or two short visits to his nestlings in the secondary nest B (Fig. 1), before returning to the fledglings from his primary nest. On the morning of fledging day at his secondary nest B, only his mate was observed feeding the three new fledglings. M1 spent most of his time about 100 m from his secondary nest, where he was probably feeding fledglings from his primary nest. Twice on that morning M1 came within a few meters of his secondary nest female, but we never saw him feed any of these new fledglings.

M2 fed two fledglings from his secondary nest from the day they fledged until we stopped observing him, two days after his tertiary nest fledged young. The female and at least one fledgling were being fed by the male at this nest on fledge day, but were not subsequently observed. As with M1's brood, the location of M2's fledged young gradually shifted toward his tertiary nest. Three days later, when the tertiary nest fledged young, we observed M2 feeding his two new fledglings while continuing to feed his two older ones from his secondary nest. On the following day we could account for only the four fledglings being fed by this same male.

Other cases of polygyny and polyterritorial advertisement.—Polyterritorial polygyny such as that of M1 and M2 are not isolated incidents in redstarts, as illustrated by a variety of less detailed examples, all involving older males. The first likely case of polygyny occurred in 1985, when a male was seen advertising and traveling with a female while she was building a nest on 7 June. We saw no other male at this nest site prior to 28 June, when this nest was depredated, but we saw this same color-banded male feeding young on the day they fledged (June 27) at a concurrent successful nest almost 200 m away (across the territory of another

redstart pair) from the depredated nest. We observed circumstances suggestive of two cases of polygyny in 1988 besides those involving M1 and M2. In the first instance, the male repeatedly left a nest site where he was feeding young, and traveled about 200 m to another site where he used advertisement song (much as M1 did when traveling to his secondary nest site); we also saw a female redstart and fledglings at this site, but were unable to confirm feeding of young here by this male. In the second case, intensive observations at the nest of one male revealed repeated periods during which he was absent from the nest site as though he were off at another nest or territory site. In 1989 we confirmed one case by observing an older male feeding a recently fledged young near the ground, fewer than 10 m away from a tree containing young (<four days old) chicks that this same male was helping to feed. We do not know where this lone fledgling came from, but certainly not from this nest, so that we think the simplest explanation is that this male had a secondary nest. In 1990 we confirmed two more cases by observations of banded males feeding nestlings at different nests. In the first case, the male alone fed four nestlings during the two days the nest was under observation until the chicks fledged on 1 July. This same male was subsequently seen feeding nestlings at a second nest found on 4 July, and depredated two days later. This second nest, on which a female must have been incubating eggs by 23 June to have nestlings hatched by 4 July, was 270 m from the first nest, and was located where this male had been observed courting a female on two different days starting on 8 June. In the second 1990 case, the male defended one relatively large (ca 1.25 ha) territory within which he helped feed young that fledged a first nest on 24 June. A second female built a nest in this territory 120 m from the first nest, began incubating on 20 June, began feeding chicks with the male's assistance when the first chick hatched on 4 July, and then abandoned the area when the nest was depredated on 5 July.

In addition to these cases of polygyny, we have observed numerous instances in which a male behaved as though he were trying to attract a second mate in a territory far removed from the primary one. One older male in 1986, and another in 1987 each advertised over 150 m from an active nest site at which each later fed young. In two instances in 1988 we observed older males advertising unsuccessfully up to 200 m away from their primary nest sites, then reverting within several minutes to serial mode song back at the primary nest site. In 1989 we observed an older male advertising in a secondary area with repeat mode song 450 m away from the site of an active nest where he had advertised and attracted a mate earlier in the season. In 1990 we observed two cases. First, a yearling male used advertisement displays on two different days in an

area approximately 415 m from the site of a nest at which it was later feeding nestlings. Second, an older male was seen repeatedly with a female at one site, then was subsequently observed advertising 150 m away to a second female on 2 June, the day this second female started to build a nest. The male shuttled between the two sites at least four times while under observation on this date. We also observed intensive female-female aggression at this second display site at 09:10 in the morning and again at about 12:00–12:44 h, when we observed extensive chases, aerial grapples, and fluttering descents of the two females to the ground. The female observed initiating nest-building never returned to this nest-site following the female-female aggression, but instead moved about 75 m further away from the primary site from which the male was shuttling initially, and built a nest there. We hesitate to call this latter example polygyny since we never confirmed that the first female nested.

DISCUSSION

The advertising behavior and occasional polygyny that we have observed in American Redstarts is remarkably similar to polyterritoriality described in the Wood Warbler (*Phylloscopus sibilatrix,* Temrin et al. 1984; Temrin 1986, 1989) and the Pied Flycatcher (*Ficedula hypoleuca,* Alatalo et al. 1981, 1982; Slagsvold and Lifjeld 1988). Monogamously mated Wood Warblers, for example, differed from unmated males in their song types and rates, with rates decreasing once mating occurred (Temrin 1986). By the time their first mates began laying, some Wood Warbler males established secondary territories within which the males resumed "unmated" song mode (Temrin et al. 1984). In both the Wood Warbler and Pied Flycatcher, secondary territories were generally not farther than a few hundred meters from primary ones, thus facilitating their defense by one male (Slagsvold and Lifjeld 1988). Similarly, redstart display territories and nests were usually at least 200–300 m apart, but occasionally up to 500 m apart (Fig. 2), with large expanses of intervening forest within which males did not display vocally. Finally, young of secondary mates in a variety of species received less parental care than those of primary mates (Alatalo et al. 1982, Temrin et al. 1984, Searcy and Yasukawa 1989, Lifjeld and Slagvold 1989). Male redstarts, however, did not completely abandon secondary mates, as did Wood Warblers (Temrin et al. 1984) and male Red-winged Blackbirds (*Agelaius phoeniceus*) in some populations (Searcy and Yasukawa 1989, Whittingham 1989). Two-year-or-older males were involved in all but one case of polygyny or polyterritorial advertising behavior we observed in Redstarts, implying that older males are more likely than yearlings to be polygynous, much as in the Pied Flycatcher (Alatalo et al. 1981, 1982). However, we observed one

yearling male displaying polyterritorially, and Reid and Sealy (1986) observed a polygynous yearling Yellow Warbler (*Dendroica petechia*).

Although we have confirmed only six cases of polygyny, regular polyterritorial advertisement behavior and several other instances of likely polygyny suggest that the phenomenon was not infrequent, occurring in about 5–15% of males in the period 1988–1990. Polygyny may have gone undetected in our study until 1988 (even though a large number of color-banded males were under observation beginning in 1983) because we became more efficient at detecting it, but it may have been unusually frequent in the period 1988–1990 (see below). American Redstarts are thus best characterized by "facultative polygyny" (Ford 1983:340), in which males of a primarily monogamous species are polygynous whenever ecological or social circumstances allow it. We are not surprised to observe polygyny in redstarts, given their plumage sexual dimorphism and male plumage bimaturism, and given the association of these characteristics with polygyny in other birds (Rohwer et al. 1980, 1983).

Why are redstarts polygynous? We find no evidence in redstarts, as in all other birds studied to date, that male-coercion of females into polygynous relationships is possible, especially in forested habitats, implying that female-choice is more likely than male-choice (Searcy and Yasukawa 1989). We also note that the polyterritorial form of polygyny in redstarts, just as in Pied Flycatchers and Wood Warblers, precludes harem size-related benefits such as added defense against nest predators seen in Red-winged Blackbirds (Searcy and Yasukawa 1989). Redstart females that join an already mated male do risk receiving decreased male effort feeding nestlings (Table 1), and so there appears to be a net cost of polygyny to such females. The "skewed-sex-ratio" model, which conceives of females mating polygynously owing to the unavailability of monogamous males, does not apply to redstarts, because floating unmated males are generally available (Morris and Lemon 1988; Sherry and Holmes 1989; Sherry, unpubl. data). We are left with two possible models: (1) The compensation, or "polygyny-threshold" model, in which females are compensated by better reproduction when mating with older males, either because of higher quality territories held or higher genetic quality of the males; and (2) a "no-compensation model" (Searcy and Yasukawa 1989). The polygyny-threshold model could apply to redstarts, since females could easily use plumage differences to distinguish between yearling and older males, and since yearling males tend on average to advertise territories in poorer habitats than older males (Sherry and Holmes 1988, and unpubl. data; but see Morris and Lemon 1988). Also, habitats vary patchily at Hubbard Brook (Sherry and Holmes 1985), in such a way that older males could monopolize the preferred, deciduous habitats (Sherry and Holmes 1989),

facilitating polygyny if females tend to become concentrated in relatively preferred habitats (Wesolowski 1987). However, yearling males appear to care for young and fledge them as successfully as older males (Procter-Gray and Holmes 1981; Morris and Lemon 1988; Omland and Sherry, unpubl. data), and so females should gain little advantage by mating preferentially with an older male. Finally, aspects of Searcy and Yasukawa's (1989) "no-compensation" model would seem to apply to redstarts and explain aspects of polygyny in this species: There could well be a search cost to females traveling through large areas of forest trying to locate mates during a short breeding season, in which clutch size declines each year (Sherry, unpubl. data). The polyterritorial form of polygyny in redstarts also allows for the possibility that females are deceived about the mating status of males, as appears to be the case in Pied Flycatchers (Lifjeld and Slagsvold 1989, Searcy and Yasukawa 1989). Our observation of redstart female-female aggression suggests that primary females may suffer when their mates establish secondary mating relationships, perhaps because primary females lose the help feeding their own nestlings that their mates provide at secondary nests (Table 1). Primary female Pied Flycatchers receive less help feeding nestlings from a polygynous than a monogamous mate (Lifjeld and Slagsvold 1989), and their aggression towards other females provides an explanation for why males display secondary territories far from primary ones, i.e., are polyterritorial (Breiehagen and Slagsvold 1988). However, female-female aggression also occurs on territories of polygynous Yellow Warblers, which are not polyterritorial (Hobson and Sealy 1989).

We are puzzled by the fact that none of the earlier studies of redstarts have observed polygyny, given its frequency at Hubbard Brook. Several explanations are possible. First, polygyny is probably difficult to detect in species such as redstarts with home-ranges occupying many hectares of heavily forested habitat, particularly when males are not color-banded. Second, relatively high nesting success of Hubbard Brook redstarts in the late 1980s (Sherry and Holmes, in press) may have facilitated confirmation of polygyny via detection of male parental care at multiple simultaneously active nests. Third, polygyny may be more frequent in some populations than others. Polygyny may have been relatively prevalent at Hubbard Brook in the late 1980s, for example, due to peculiar ecological circumstances. The redstart population at Hubbard Brook in the period 1988–1990 was at its lowest abundance since we began mapping territories in 1981 in our 180-ha area (Sherry and Holmes, in press), and the population on a 10-ha part of the 180-ha area was as low in 1988 as anytime in the previous 18 years (Holmes and Sherry 1988). Low abundance would have facilitated males' uncontested movement within suitable habitat, and all six cases of confirmed or likely redstart polygyny involved territories

connected by unoccupied corridors of appropriate deciduous habitat (e.g., Fig. 2). Moreover, the low-abundance populations in 1988–1990 were comprised disproportionately of yearling males (Sherry and Holmes, in press), and presumably also of yearling females. Older males might have experienced decreased competition for mates from the relatively few older males and from the less experienced yearling males (which are generally unsuccessful in competition with older males for territories and mates—Sherry and Holmes 1989). The secondary female of male M1 and the tertiary female of M2 were both almost certainly yearling females, which are likely to be inexperienced at assessing mating status of males (see, e.g., Alatalo et al. 1981). Since American Redstarts appear to be invariably single-brooded at Hubbard Brook (T. W. Sherry, unpubl. data), our observations are consistent with the hypothesis of Slagsvold and Lifjeld (1988) that polyterritorial polygyny is promoted by conditions of low intraspecific competition for mates in single-brooded species with a short reproductive season.

In conclusion, our data and observations suggest that polygyny in American Redstarts results from a facultative strategy used primarily by older males to increase mating opportunities in a female-mate-choice system. Polygynous matings in redstarts appear to be facilitated both by males' locating secondary territories far from primary nesting sites, i.e., polyterritoriality, and by relatively low levels of intraspecific competition among males for mates. Secondary females received less assistance from males feeding nestlings than primary females, and an instance of female-female aggression suggests that primary females may attempt to restrict polygynous matings by their mates. To our knowledge this is the first reported case of polyterritorial polygyny in a North American bird.

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NEOTROPICAL MIGRANT BIRDS AND EDGE EFFECTS AT A FOREST-STREAM ECOTONE

J. Edward Gates and Neil R. Giffen[1]

Abstract.—Species richness, density, and avian diversity were examined along a deciduous-coniferous forest gradient from a ridge crest to a stream bottomland. The study was conducted in Garrett County, Maryland, a region in the central Appalachian Mountains that is 71.2% forested. The 35-ha study area was within a 270-ha core of continuous forest. Bird species were located and habitat sampled using a 35 × 35-m grid that covered a 77-m elevational gradient from a small, second-order stream to a ridge top. Later, twenty-three, 30-m wide elevational bands of 1.26 ha each were defined to relate bird and habitat attributes. Principal components analysis reduced 23 habitat variables to three principal components and provided an ordination of the 23 elevational bands. Four vegetative zones were identified along the main deciduous-coniferous gradient of PC-I, the deciduous zone on the ridge crest, followed by a deciduous/sparse hemlock zone, a hemlock/deciduous zone further downslope, and a hemlock/rhododendron zone at the stream. Based on polynomial regression, the fewest numbers and species of birds were found in the deciduous zone on the ridge. More species occurred with the addition of hemlock at the deciduous-deciduous/sparse hemlock ecotone and markedly more with the addition of rhododendron at the hemlock/rhododendron-stream edge, where rhododendron and total short shrub cover were the highest and deciduous and total canopy cover and deciduous basal area were the lowest. Of 28 breeding bird species, 60.7% were neotropical migrants representing 82.5% of all birds recorded on the study area. Neotropical migrants concentrated near the forest-stream edge as many edge or mixed-habitat species do at forest-field edges. High numbers of cowbirds near the forest-stream edge likely posed a serious threat to these breeding neotropical migrants. These data suggest that conditions at certain forest-stream edges might be conducive to increased nest predation and cowbird parasitism within forested landscapes minimally fragmented by human activities. *Received 2 Oct. 1990, accepted 21 Feb. 1991.*

Breeding bird species richness and density generally are high near edges of forests, particularly at abrupt, shrubby, forest edges bordering fields or other openings (Gates and Gysel 1978, Strelke and Dickson 1980, Chasko and Gates 1982, Morgan and Gates 1982, Hansson 1983). This high diversity reflects the greater number and percent coverage of vegetative strata at these forest edges (MacArthur and MacArthur 1961, MacArthur et al. 1962) and often leads to a high nest density, primarily of edge or mixed-habitat species (Gates and Gysel 1978, Chasko and Gates 1982). Certain human-made forest edges have been characterized as ecological traps for open-nesting passerines, because high numbers of nests near these edges result in high nest mortality from predation and cowbird parasitism (Gates and Gysel 1978). Increase in edge and loss of habitat

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resulting from forest regeneration and fragmentation may reduce reproductive success of many neotropical migrants, particularly those bird species specialized for breeding in mature forest interiors (Wiens 1989).

Bodies of water have been described as openings in forests that lead to changes in the physical and biotic characteristics of the interior, but their effect is not thought to be as great as terrestrial openings (Small and Hunter 1988). Few studies, however, have investigated the potential of riparian ecotones to have a detrimental effect on breeding birds of the forest interior. A major landscape feature of the central Appalachians is the dendritic patterns of streams penetrating the forest interior. Streams could function similarly to human-made corridors within forested landscapes for the birds nesting there. The objectives of this study were (1) to determine whether or not there is a greater bird species diversity near the forest-stream edge than within the interior of a minimally fragmented forested landscape, (2) to determine the composition of the bird assemblage near the forest-stream edge, (3) to ascertain what bird assemblage attributes are associated with the vegetative structure, and (4) to evaluate if conditions at the forest-stream edge are conducive to the formation of ecological traps for birds.

STUDY AREA AND METHODS

The study area was located in a 270-ha core of continuous forest in Garrett County, Maryland, on the watershed of the City of Frostburg (see Gates and Harman 1980). Adjacent habitats included extensive forest to the north, west, and south; and cultivated fields and pasture to the east. Human-made corridors bordering the core area included a 6.1-m-wide county road to the north, with about a 3-m unmowed, grass strip on either side; a 5.2-m-wide access road to the reservoir of the City of Frostburg to the west; and a 9.8-m-wide waterline/powerline corridor to the south. The county is 71.2% forested with clearings in crops (10.0%); pasture (6.9%); other farmland (3.3%); and other land (8.6%), e.g., clear-cuts, corridors, etc. (Frieswyk and DiGiovanni 1988).

The core study area was a mature, northern-hardwood forest community. Sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), northern red oak (*Quercus rubra*), cucumber magnolia (*Magnolia acuminata*), and black cherry (*Prunus serotina*) occupied the ridge crest and slope; while along the stream bottomland American hemlock (*Tsuga canadensis*), yellow birch (*Betula lutea*), and red maple (*Acer rubrum*) predominated (Gates and Harman 1980). Blandy Run, a 3.4-m wide, second-order stream flowing generally southeast-northwest, formed a natural corridor and divided the study area into a northern section (approx. 75% of the study area) and a southern section (25%). The stream was bordered by a dense thicket of rosebay rhododendron (*Rhododendron maximum*), an evergreen shrub. Elevations ranged from 740 m at the stream to 817 m on the ridge crest. Soils were loam (0–35% slopes) and silt loam (3–8% slopes), with alluvial soil along Blandy Run (Stone and Matthews 1974). The climate is temperate continental with July (19.8°C) and January (−2.9°C) being, on average, the hottest and coldest months of the year. The average annual precipitation is 114 cm.

The surveyed area totaled 35 ha (420 × 840 m) and was gridded with stake-wire flags set at 35-m intervals. The grid covered a 77-m elevational gradient extending from the stream

to the ridge crest and was used in locating bird species and habitat sampling points. Later, the area was divided into twenty-three, contiguous 30-m wide elevational bands with the 420-m axis paralleling the stream. Each band was approximately 1.26 ha, with 19 such bands north and four south of the stream. To reduce edge effects, elevational bands were located at least 100 m from openings other than at the stream, resulting in loss of six ha from the surveyed area. The area was surveyed eight times for breeding bird species between 25 May and 15 July 1981. Birds were located on gridded cover maps of the surveyed area (Kendeigh 1944). A count was begun immediately after sunrise and completed within 4.5 h. Random sampling of habitat variables occurred at two hundred and ninety-six grid intersections. On average, 12.9 (range = 9–17) intersections were located in each band, with 19 bands having 11–14. An ocular tube was used to estimate percent coverage (20 ± readings/intersection, + = contact with a vegetative stratum) of the different vegetative strata: herbaceous, evergreen, and total ground cover; rhododendron, hemlock, deciduous, and total short (>0–1.7 m in height) and tall (>1.7–4.6 m in height) shrub cover; and hemlock, deciduous, and total understory (>4.6–12 m in height) and canopy (>12 m in height) cover. Hemlock, deciduous, snag, and total basal area (m^2/ha) were determined at each point with an angle gauge. Elevation (m) was estimated with a surveying altimeter, and distance (m) from the stream was measured with a tape.

The environmental gradient in the habitat data was examined using principal components analysis (PCA) ordination (SAS Institute 1985, Ludwig and Reynolds 1988). Detrended principal components (DPC) analysis was used to examine nonlinearity, or if any arching pattern existed as a result of relationships among the habitat variables (Ludwig and Reynolds 1988). DPC can be used to detrend the arch into one axis to reflect the underlying environmental gradient. The values of the different habitat variables within the 23 elevational bands were first checked for normality and then transformed, if necessary, before PCA was performed. To interpret the underlying environmental gradient represented by each PC, the habitat variables were correlated with each PC using Pearson product-moment correlation.

Bird species richness, i.e., the cumulative number of species identified over the eight counts; density, i.e., the mean number of bird observations per count; and the index of bird species diversity (Shannon-Wiener index, H') and evenness (J') were calculated for each 1.26-ha elevational band (Ludwig and Reynolds 1988). The relationships of these values to PC-I and II were determined using polynomial regression analysis. Coefficients of determination (R^2) were calculated for the polynomial curve having the best fit to the data. Density of individual bird-species observations per elevational band also was correlated with PC-I, II, and III to determine the relationship between those observations and the environmental gradient on the study area.

RESULTS

The first three PC's accounted for 77.8% of the total variation in the habitat data correlation matrix, with PC-I accounting for 56.4% (Table 1). Ordination with and without the variables elevation and/or distance from stream gave similar results. DPC produced a non-significant (F ratio = 1.695, df = 2/20, $P > 0.05$) parabolic regression, indicating that the original PCA axes I and II cannot be combined into a single detrended principal component axis; therefore, both PC-I and II were examined separately. Correlation analyses of the original habitat variables with the PC's demonstrated that PC-I represented a deciduous-coniferous forest gradient from the northern hardwood upland to the predominantly hem-

TABLE 1

RESULTS OF PRINCIPAL COMPONENTS AND CORRELATION (*r*) ANALYSES OF HABITAT VARIABLES (N = 23) WITH PC-I, II, AND III

	PC-I	PC-II	PC-III
Eigenvalue	12.965	2.764	2.170
Relative % of the total variance accounted for by the PC's	56.4	12.0	9.4
Cumulative % of total variance accounted for by the PC's	56.4	68.4	77.8
Correlation of habitat variables with the PC's			
Ground cover (%)			
Herbaceous	0.786***	0.288	0.048
Evergreen	0.399	−0.036	0.475*
Total	0.821***	0.313	0,125
Short shrub cover (%)			
Rhododendron	0.746***	−0.458*	−0.220
Hemlock	0.721***	0.012	0.497*
Deciduous	−0.784***	−0.203	0.436*
Total	−0.044	−0.640***	0.577**
Tall shrub cover (%)			
Rhododendron	0.792***	−0.380	−0.208
Hemlock	0.935***	0.075	0.236
Deciduous	−0.954***	−0.141	0.083
Total	−0.617**	−0.390	0.279
Understory cover (%)			
Hemlock	0.885***	0.196	−0.173
Deciduous	−0.964***	−0.059	0.118
Total	−0.789***	0.001	−0.050
Canopy cover (%)			
Hemlock	0.727***	−0.008	−0.128
Deciduous	−0.472*	0.691***	0.436
Total	−0.275	0.781***	0.410
Basal area (m^2/ha)			
Hemlock	0.918***	0.073	0.251
Deciduous	−0.575**	0.568**	−0.252
Snag	0.689***	−0.164	−0.088
Total	0.784***	0.334	−0.346
Elevation (m)	−0.892***	0.019	−0.338
Distance from stream (m)	−0.901***	0.027	−0.369

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

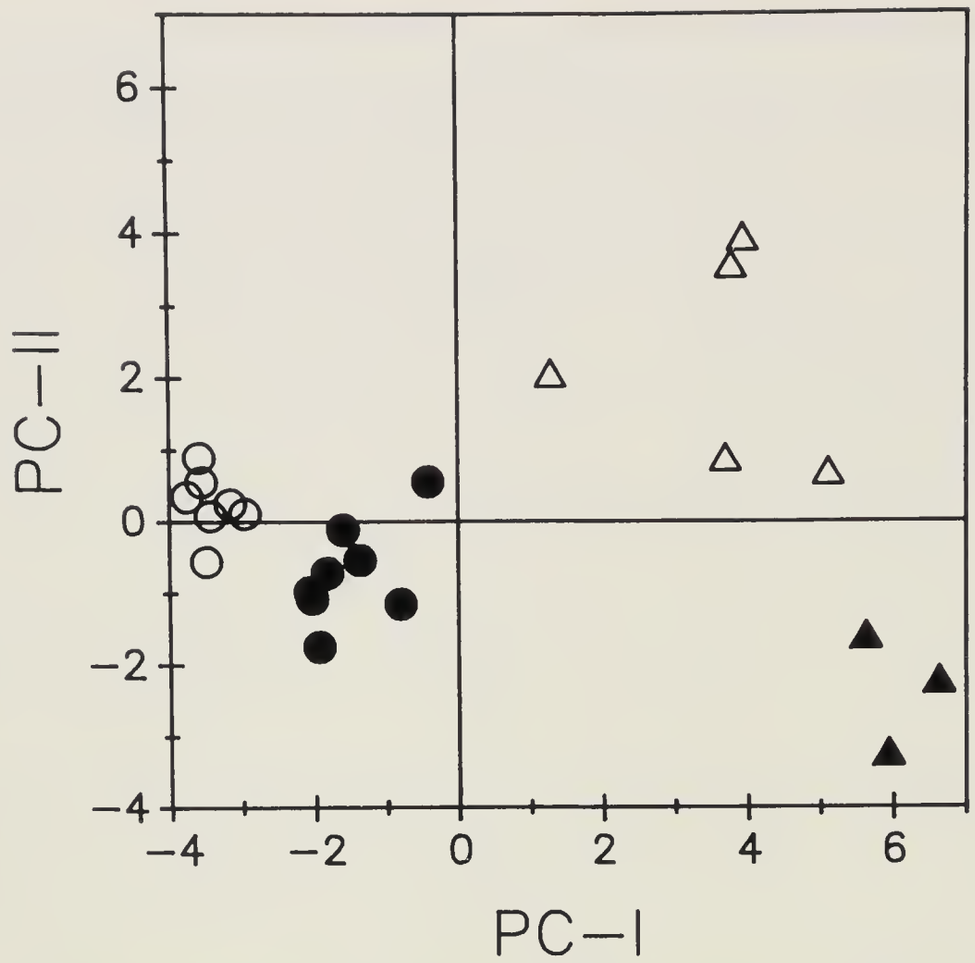

FIG. 1. Principal components ordination of 23 elevational bands within a northern hardwood forest in western Maryland. The deciduous-coniferous forest gradient was partitioned into four vegetative zones; deciduous (open circle), deciduous/sparse hemlock (solid circle), hemlock/deciduous (open triangle), and hemlock/rhododendron (solid triangle).

lock bottomland along Blandy Run (Table 1). This deciduous-coniferous gradient was superimposed on the elevation/moisture gradient. Along the deciduous-coniferous gradient, four vegetative zones, two deciduous and two coniferous, were delineated based on field observations of similarities as well as clustering of elevational bands along PC-I (Fig. 1). A deciduous zone on the ridge crest (approximately 360–690 m from the stream) had the lowest ground cover and the highest deciduous cover and basal area. Continuing downslope toward the stream (120–360 m away), a deciduous/sparse hemlock zone contained more ground cover, higher hemlock shrub cover, and high deciduous cover and basal area. A hemlock/deciduous zone located farther downslope (60–120 m from the stream) was characterized by less deciduous and more hemlock and rhododendron shrub cover, and a decrease in deciduous cover and basal area with a corresponding increase in that of hemlock. Finally, a hemlock/rhododendron zone nearest the stream (0–60 m) was characterized by high ground cover, high rhododendron and hemlock cover, and high hemlock and snag basal area. Observable ecotones occurred between the deciduous and decidu-

ous/sparse hemlock zones with the addition of hemlock, and between the hemlock/rhododendron zone and the stream with the addition of streamside rhododendron shrub cover. PC-II separated the two coniferous zones and was a measure of certain deciduous patches within the coniferous portion of the gradient that were characterized by low rhododendron and total short shrub cover, and high deciduous and total canopy cover and deciduous basal area. PC-III represented other patches of high evergreen ground cover and hemlock, deciduous, and total short shrub cover.

The three measures, species richness, density, and diversity index, used to characterize the breeding bird assemblage were strongly associated with PC-I and II based on polynomial regression analyses. Using sequential sums of squares to determine when additional polynomial terms were unnecessary, the cubic polynomial curve was found to provide the best fit of the data to PC-I (Fig. 2). The bird assemblage was most sparse in the deciduous zone on the ridge, increased with the addition of hemlock at the ecotone and markedly increased with the addition of rhododendron at the forest-stream edge. Evenness showed a slight linear relationship ($R^2 = 0.20$, $P < 0.05$) with PC-I, indicating that observations of species were more equitable near the stream. A quadratic polynomial curve provided the best fit of species richness and diversity index to PC-II; however, a cubic polynomial curve gave a slightly better fit of density of bird observations to PC-II (Fig. 3). The highest values occurred within the coniferous zones, particularly where rhododendron and total short shrub cover were the highest, and deciduous and total canopy cover and deciduous basal area were the lowest. There was no relationship ($R^2 = 0.001$, $P > 0.05$) of evenness with PC-II.

Of the 28 breeding bird species, 60.7% were neotropical migrants (Whitcomb et al. 1981, Robbins et al. 1989) representing 82.5% of the total number of birds recorded on the study area. Seventeen species occurred in sufficient numbers (≥nine observations) and across enough elevational bands (≥4) to make correlation analysis worthwhile (Table 2). Those neotropical migrants found on only one elevational band or occurring in low numbers included Great Crested Flycatcher (*Myiarchus crinitus*), Hooded Warbler (*Wilsonia citrina*), Black-and-white Warbler (*Mniotilta varia*), Northern Waterthrush (*Seiurus noveboracensis*), and Louisiana Waterthrush (*Seiurus motacilla*). Resident/short distance migrants that also were infrequently observed included Pileated Woodpecker (*Dryocopus pileatus*), American Crow (*Corvus brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), Cedar Waxwing (*Bombycilla cedrorum*), Common Yellowthroat (*Geothlypis trichas*), and Mourning Dove (*Zenaida macroura*). Based on correlation analysis, two main groups of neotropical migrants were identified; one associated with the deciduous upland and another asso-

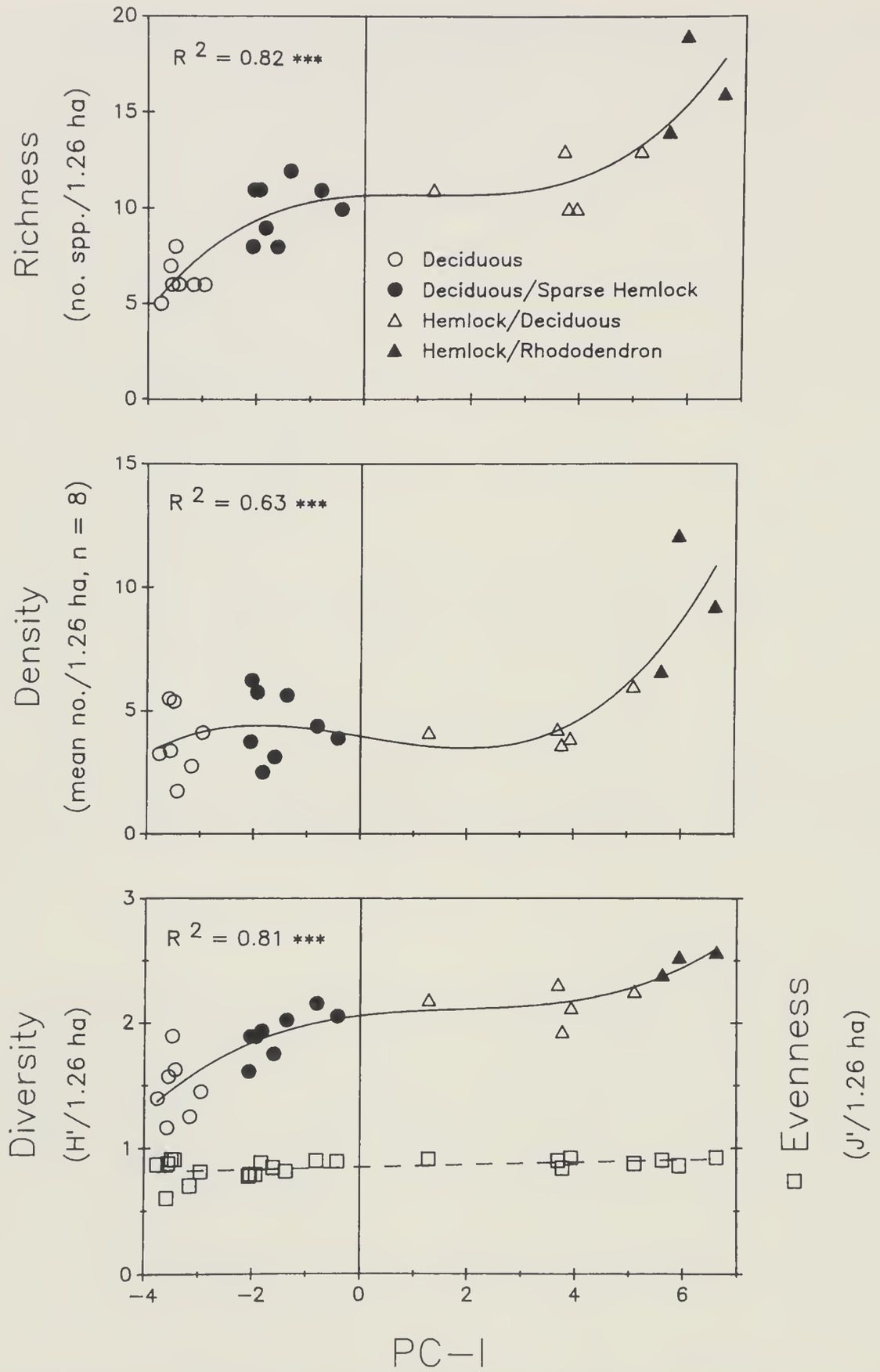

FIG. 2. The association of the bird assemblage attributes of species richness, density, and diversity with PC-I determined by polynomial regression (*** $P < 0.001$).

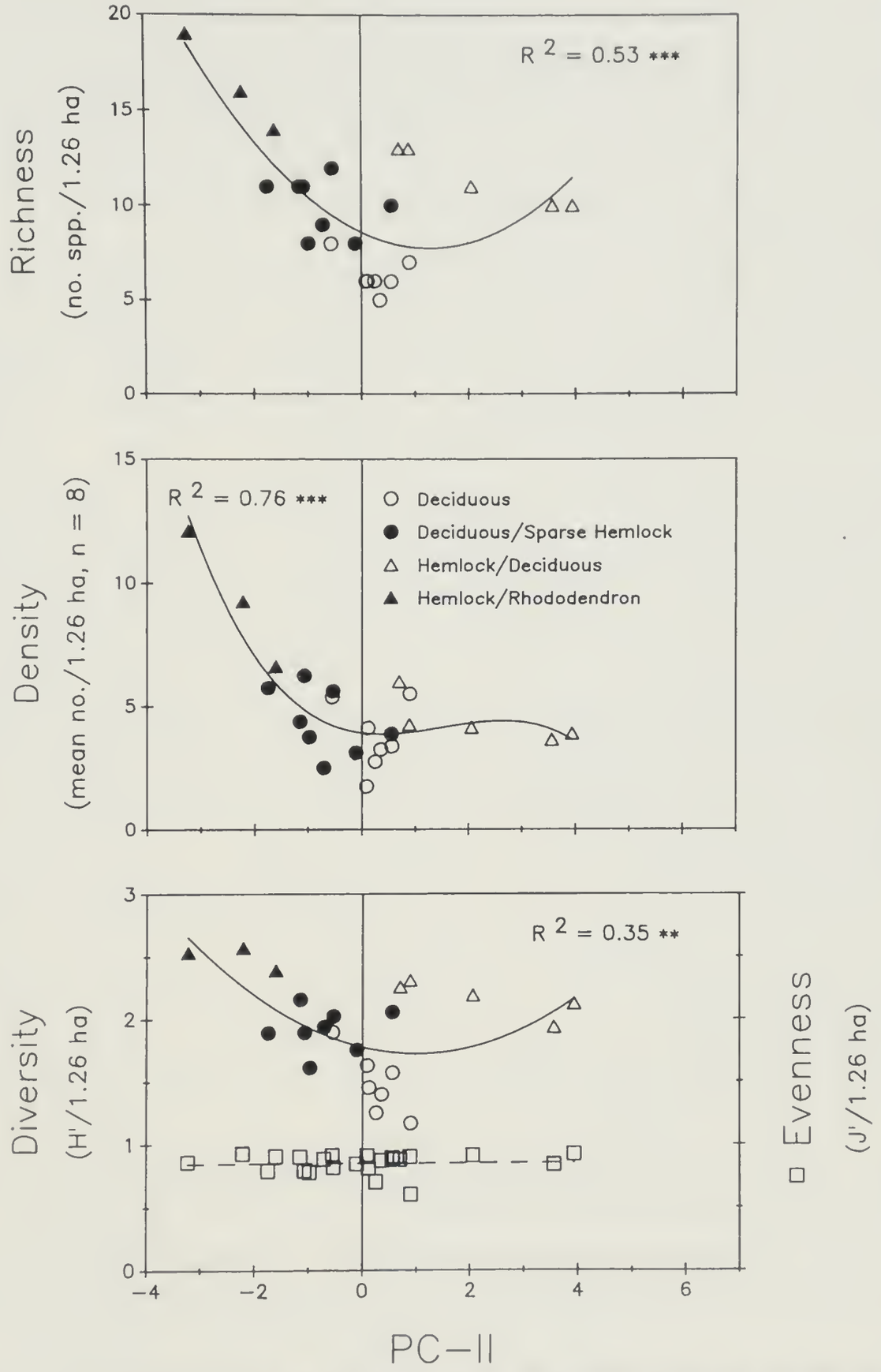

FIG. 3. The association of the bird assemblage attributes of species richness, density, and diversity with PC-II determined by polynomial regression (** $P < 0.01$, *** $P < 0.001$).

TABLE 2

CORRELATION (*r*) ANALYSIS OF DENSITY OF BIRD SPECIES OBSERVATIONS (MEAN NUMBER PER 1.26 HA, N = 8) WITHIN EACH ELEVATIONAL BAND (N = 23) WITH PC-I, II, AND III

	PC-I	PC-II	PC-III
Neotropical migrants			
Eastern Wood-Pewee (*Contopus virens*)	−0.775***	−0.258	−0.127
Acadian Flycatcher (*Empidonax virescens*)	0.392	−0.550**	0.286
Veery (*Catharus fuscescens*)	0.509*	−0.182	−0.267
Wood Thrush (*Hylocichla mustelina*)	0.691***	−0.336	0.116
Red-eyed Vireo (*Vireo olivaceus*)	−0.660***	−0.116	−0.138
Solitary Vireo (*V. solitarius*)	0.933***	0.016	−0.015
Black-throated Green Warbler (*Dendroica virens*)	0.287	0.136	−0.036
Black-throated Blue Warbler (*D. caerulescens*)	0.456*	−0.463*	0.056
Canada Warbler (*Wilsonia canadensis*)	0.723***	−0.544**	−0.292
Nashville Warbler (*Vermivora ruficapilla*)	0.689***	−0.520*	−0.242
Ovenbird (*Seiurus aurocapillus*)	0.333	0.216	0.489*
Scarlet Tanager (*Piranga olivacea*)	−0.435*	−0.277	−0.382
Resident/short distance migrants			
Hairy Woodpecker (*Picoides villosus*)	0.391	−0.386	−0.261
Black-capped Chickadee (*Parus atricapillus*)	0.638**	−0.371	−0.208
Tufted Titmouse (*P. bicolor*)	0.313	−0.140	0.344
White-breasted Nuthatch (*Sitta carolinensis*)	−0.395	0.186	−0.004
Brown-headed Cowbird (*Molothrus ater*)	0.576**	0.254	0.274

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

ciated with the hemlock bottomland (Table 2). The deciduous upland group included the Eastern Wood-Pewee, Red-eyed Vireo, and Scarlet Tanager (scientific names appear in Table 2, if not given in text); the hemlock bottomland group included the Veery, Wood Thrush, Solitary Vireo, Black-throated Blue Warbler, Canada Warbler, and Nashville Warbler. The Acadian Flycatcher and Ovenbird were associated with particular patches along the deciduous-coniferous gradient. The Acadian Flycatcher was more abundant in areas near the stream characterized by high amounts of rhododendron and total short shrub cover, but with low deciduous and total canopy cover and deciduous basal area. These areas were generally open in the middle vegetative strata. The Ovenbird was

more abundant where evergreen ground cover and hemlock, deciduous, and total short shrub cover were high. These patches provided high amounts of cover near the ground. The Black-throated Green Warbler was not significantly associated with any of the PC's. The resident/short distance migrants also were typically not associated with any of the PC's. The Black-capped Chickadee and Brown-headed Cowbird were recorded more frequently in the hemlock/rhododendron vegetative zone. Cowbird numbers within the hemlock/rhododendron zone were 1.27 times higher than that in the hemlock/deciduous zone and 4.14 times higher than that in the deciduous/sparse hemlock zone. At >240 m from the stream and within the deciduous zone, they were essentially absent.

DISCUSSION

Although edge effects are often considered an anathema to neotropical migrants, the high values of richness, density, and diversity near the forest-stream edge were due to the presence of breeding neotropical migrants, most of which are characterized as forest-interior or area-sensitive species (Whitcomb et al. 1981, Robbins et al. 1989). Regression of the three attributes of the bird assemblage on PC-I demonstrated the importance of the deciduous-deciduous/sparse hemlock ecotone and then the hemlock/rhododendron-stream edge to the overall pattern. Compared to the adjacent deciduous forest, the increase in coverage of vegetative strata, particularly that of evergreens; horizontal vegetative patchiness resulting from canopy gaps formed by dead trees, i.e., snags; and moisture near the stream likely resulted in a more varied and productive habitat with many foraging and nesting substrates (Wiens 1989).

The natural forest-stream edge had certain characteristics in common with some edges created by human disturbance, e.g., forest-field and forest-powerline corridor edges (Gates and Gysel 1978, Chasko and Gates 1982). Although not to the extent found at some human-made edges, the contrast at the hemlock/rhododendron-stream edge was high, and the width as characterized by the rhododendron shrub border was generally narrow. However, the forest-stream edge was sinuous rather than linear. The dense border of shrubby vegetation was similar between forest-stream and forest-field edges contributing to the "edge wall" of foliage formed by many vegetative layers. Furthermore, bird assemblages at forest-field and forest-corridor edges are dominated by edge or mixed-habitat species; whereas forest-interior birds contributed to the edge effect at the forest-stream edge (Gates and Gysel 1978, Chasko and Gates 1982).

Given these vegetative characteristics, we might predict that birds nesting near the forest-stream edge would suffer comparable high mortality as birds near similarly structured forest-field and forest-corridor edges.

Predator activity is often concentrated at the interface between adjacent habitats (Bider 1968, Gates and Gysel 1978, Chasko and Gates 1982, Gates, 1991). Streams also concentrate predator activity and are frequently used as travel corridors by mammals, e.g., raccoon (*Procyon lotor*) and mink (*Mustela vison*) (Harris 1984, Forman and Godron 1986, Gates, pers. obs.). Additionally, predators increase their search intensity in response to discovering occupied nests (Martin 1988). However, birds nesting in large patches of vegetation, e.g., rhododendron thickets, may have higher nesting success than those nesting in smaller habitat patches, e.g., isolated rhododendron shrubs; because, the number of potential nest sites that predators must search would be greater in larger patches (Chasko and Gates 1982, Martin and Roper 1988, Møller 1988). Additionally, if the edge is wide enough, birds may be able to disperse their nests, thereby reducing the probability of a chance encounter with a nest predator.

Besides potential impacts from predators, known impacts on breeding neotropical migrants come from two disparate sources. Expansion of the breeding range and populations of the Brown-headed Cowbird have been associated with declines of populations of neotropical migrants (Brittingham and Temple 1983, Wiens 1989). The higher number of Brown-headed Cowbird observations near the hemlock/rhododendron-stream edge was noteworthy, as cowbirds are habitat generalists, and their presence is dependent upon host-nest density (McGeen 1972). The abundance of snags near the hemlock/rhododendron-stream edge as well as canopy gaps serve as attractants to cowbirds (Brittingham and Temple 1983, Robbins et al. 1989). Because forest habitat does not provide sufficient open foraging sites for this ground-foraging bird, cowbirds utilizing forest interiors often maintain separate breeding and foraging ranges (Brittingham and Temple 1983). Foraging areas in nearby open fields and clearings allow cowbirds to penetrate deeply into forest interiors and utilize even small canopy openings as sites from which to parasitize nests of forest-interior birds. Susceptibility is known to be high among the neotropical migrant species nesting near the hemlock/rhododendron-stream edge (Friedmann 1963, 1971; Brittingham and Temple 1983; Gates, pers. obs.).

We noted an even more insidious threat to neotropical migrants breeding in the hemlock/rhododendron zone: habitat alteration by white-tailed deer (*Odocoileus virginianus*) (Alverson et al. 1988, Gates, pers. obs.). Deer concentrate in hemlock and rhododendron cover in the central Appalachians during severe winter weather (Gates and Harman 1980, Lang and Gates 1985). Prolonged use of this habitat leads to a browse line at about 2 m in height, below which there is little vegetation. In some localities, reproduction of hemlock and rhododendron has been completely eliminated by deer browsing (Alverson et al. 1988, Gates, pers.

observ.). Many of these neotropical migrants nest on or near the ground in open nests (Whitcomb et al. 1981). Besides immediate loss of nesting habitat and concealing nest cover, there is potential for elimination of the hemlock/rhododendron habitat type in many localities and possibly with it the associated bird assemblage. Additionally, fragmentation of rhododendron thickets by deer browsing could increase the probability of predation by reducing the number of available nest sites (Martin and Roper 1988).

In conclusion, the hemlock/rhododendron-stream edge contributed significantly to the high diversity of neotropical migrants. These birds appeared to be responding in a similar manner to the narrow, high-contrast, multi-layered edge occurring at the forest-stream interface as more typical edge or mixed-habitat species respond to narrow, high-contrast, multi-layered forest-field edges. It seems likely that no species assemblage can be classified as truly edge species; but, many birds can inhabit different edge habitats, including numerous neotropical migrants associated with forest interiors. The hemlock/rhododendron-stream edge could function as an ecological trap (Gates and Gysel 1978, McKearnan and Gates, unpubl. data); however, composition and structure of the habitat within and on either side of the edge would have a controlling influence on the bird species assemblage as well as on competitors, predators, and nest parasites by influencing distributional patterns and permeability of the edge. The forest-stream edge did lack the usual array of mixed-habitat competitors associated with shrubby forest edges. However, this result was likely due to the fact that this edge bordered a narrow stream corridor within a forested region rather than an extensive terrestrial opening.

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APPROACHES TO THE CONSERVATION OF COASTAL WETLANDS IN THE WESTERN HEMISPHERE[1]

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ABSTRACT.—Coastal wetlands rank among the most productive and ecologically valuable natural ecosystems on Earth. Unfortunately, they are also some of the most disturbed. Because they are productive and can serve as transportation arteries, coastal wetlands have long attracted human settlement. More than half of the U.S. population currently lives within 80 km of its coasts, and one estimate places 70% of all humanity in the coastal zone. Human impacts to coastal wetlands include physical alteration of hydrological processes; the introduction of toxic materials, nutrients, heat, and exotic species; and the unsustainable harvest of native species. Between 1950 and 1970, coastal wetland losses in the U.S. averaged 8100 ha/year. In Central and South America, development pressures along the coastal zone rank among the most serious natural resource problems in the region.

Here, we (1) briefly describe coastal wetland avifauna, (2) discuss the threat of global warming on coastal wetlands, (3) use several Western Hemisphere wetlands as site-specific examples of development pressures facing these habitats, and (4) provide synopses of non-governmental and governmental approaches to wetland conservation. Overall, we provide a socio-economic context for conservation of coastal wetlands in the Western Hemisphere. We suggest that efforts aimed at conserving sites of particular importance for their biological diversity should be pursued within a framework of wise use that addresses the broader issues of human population growth and economic development.

"*Ere long marshes will be looked upon by mankind as gifts from heaven to prolong the life and happiness of the greatest portion of the animal kingdom*" (A. Seybert 1799).

Coastal wetlands include seasonal and relatively permanent coastal-plain freshwater swamps and marshes, coastal beaches, rocky shorelines, estuarine salt marshes, mangrove swamps, seagrass beds, mud flats, oyster reefs, and sand bars (Figs. 1 and 2). Such habitats are usually characterized

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FIG. 1. Aerial view of a typical cordgrass (*Spartina alterniflora*) salt-marsh estuary (the North Inlet Estuary) near Georgetown, South Carolina.

as low-lying lands in which the water table is at or near the surface on a regular, albeit sometimes intermittent, basis. The Convention on "Wetlands of International Importance Especially as Waterfowl Habitat"—the so-called "Rasmar Convention"—broadly defines coastal wetlands to include ". . . areas of marine water the depth of which at low tide does not exceed six metres," (Ramsar, Article 2; Lyster 1985). Many authorities, however, include permanently flooded areas in their definition of coastal wetlands only when such sites contain emergent vegetation (Arthington and Hegerl 1988). Despite considerable variation within and among sites (Day et al. 1989), coastal wetlands, especially estuaries, rank among the most productive and ecologically valuable natural habitats on Earth (Whittaker and Likens 1971, Odum 1978).

Because of their primary and, especially, secondary productivity, as well as their value as transportation arteries, coastal wetlands have been attractive sites for human settlement for thousands of years. Many of the prominent "cradles of civilization" developed in and, initially, thrived around the coastal estuaries of the Middle East, India, and China. In California, "maritime-dependent" human settlements date from the second millennium B. C. On the East Coast of North America, fish weirs dating from 1700 B. C. have been excavated in what is now Boston, Massachusetts (Siry 1984). In most instances, developing centers of hu-

FIG. 2. The Caroni Swamp, Trinidad, West Indies. This 5600-ha mangrove swamp was once the only breeding site of Scarlet Ibises (*Eudocimus ruber*) in Trinidad.

man population substantially modified their wetland habitats. Archaeological excavations in central Greece reveal that the draining of Lake Copais dates from the 25th Century B. C. (Despite the later apocryphal attempts of Hercules to reflood the area, this 20,000-ha lake site remains completely drained [Heliotis 1988].) Similar anecdotes abound for the more recently settled Western Hemisphere, where for example, in the late 18th Century, three of the founding fathers (G. Washington, T. Jefferson, and P. Henry) of the then fledgling United States suggested draining the Great Dismal Swamp in coastal Virginia (Hair 1988).

Humanity continues to concentrate its population centers in coastal regions. In New York for example, where the statewide population averages 351 people/mile^2, density increases to more than 5000 people/mile^2 in coastal counties (Simon 1978). Currently, 52% of the U.S. population lives within 80 km of the U.S. coast (Southworth 1989); worldwide, many of our largest cities are in coastal areas (Day et al. 1989), and some estimates place 70% of the world's human population along sea coasts (cf. Cherfas 1990). As humanity continues to grow and settle in such sites, coastal wetlands face an increasingly perilous future. Humans impact coastal wetlands directly through (1) physical alteration, (2) the introduction of toxic materials, (3) enrichment with excessive levels of naturally occurring materials (including nutrients) and heat, and (4) the harvesting of native species and the introduction of exotic species (Day

et al. 1989). Potential indirect, and certainly more difficult to document, effects include saltwater intrusion and increased flooding as a result of water-use systems, channelization, and global sealevel rise (Abrahamson 1989, Lester and Myers 1989).

As a result of human impacts, many coastal wetlands in the Western Hemisphere have already been lost. Tiner (1984) suggests that only 46% of the original wetland acreage in the U.S. remains. Although most U.S. wetland losses have occurred in noncoastal sites, the loss of coastal wetlands between 1950 and 1970 is reported to have averaged 8100 ha/year (Frayer et al. 1983). Other estimates (Gagliano et al. 1981, Hefner and Brown 1985) suggest even greater declines, with the southeastern U.S. losing 7% of its coastal wetlands—mainly salt marshes—over the same two decades. Speth (1979) suggests that within the last 100 years, 70% of California's intertidal wetlands have been altered by humans.

In Latin America and in the Caribbean Basin, pressures along the coastal zone currently are among the most serious problems facing natural resource management in the region. In the face of extraordinary external debt, rising populations, and widespread poverty, governments are attempting to expand agricultural and industrial production, while local inhabitants are using resources even more intensively to meet daily needs. A recent compilation of neotropical wetlands of international importance within the context of the Ramsar Convention (Scott and Carbonell 1986) reports that almost 20% of these wetlands are threatened with draining for agricultural purposes (Maltby 1988). Unfortunately, only four of the 44 countries in the region, representing less than 20% of all neotropical wetlands, are contracting parties of the Ramsar Convention (Smart 1989, Schlatter 1989).

Recent international attempts to stem the tide of wetland loss are highlighted by (1) "The Convention on Wetlands of International Importance Especially as Waterfowl Habitat," which in 1971 became the first of four recent international treaties that currently form the basis of international wildlife law (cf. Lyster 1985); (2) the inauguration in 1985 by the International Union for Conservation of Nature and Natural Resources of a global campaign to preserve wetlands; (3) a United Nations declaration making 1986 the International Year for Wetland Conservation; and (4) the establishment of the North American Waterfowl Management Plan and the Western Hemisphere Shorebird Reserve Network.

In this report, we do not attempt to provide a thorough overview of the status and conservation of coastal wetlands in the Western Hemisphere; we leave that to more lengthy and detailed treatments of the subject (e.g., Alexander and Broutman 1986, Scott and Carbonell 1986, Feierabend and Zelazny 1987, Zelazny and Feierabend 1988, Pannier and Dickinson 1989). Instead, we focus on several issues of concern with which

we are familiar, especially as they affect the birds that inhabit these environments. Specifically, after briefly describing coastal wetland avifauna, we (1) discuss the encroaching threat of global warming on coastal wetlands and their avifauna, (2) use the Florida Everglades, the Arctic coastal plain of Alaska, and coastal wetlands in Central and South America as site-specific case studies to indicate the complexities, both biological and sociological, that face wetland conservationists, and (3) provide synopses of the Western Hemisphere Shorebird Reserve Network, the North American Waterfowl Management Plan, and government programs in the U.S. as examples of private and Federal approaches to wetland conservation.

For additional information, or to offer suggestions on any of the topics discussed herein, please contact the principal author(s) of each section: Introduction and Coastal Wetland Avifauna (Bildstein), Global Warming (Nol), Florida Everglades (Bancroft), Arctic Coastal Plain (Senner), Central and South American Coastal Wetlands (Dugan and Bildstein), Western Hemisphere Shorebird Reserve Network (Payne), North American Waterfowl Management Plan (Gordon), and U.S. Government Programs (Erwin).

COASTAL WETLAND AVIFAUNA

Less than 3% of the Western Hemisphere land surface consists of coastal wetlands. Estuarine wetlands are even less common, comprising, for example, only 0.3% of the land surface of the lower 48 states (Tiner 1984). Even so, these habitats are characterized by both high densities of birds and considerable species richness. Typically, coastal wetland avifauna is dominated, at least numerically, by large numbers of Anseriforms (waterfowl), Ciconiiforms (long-legged wading birds), and Charadriiforms (shorebirds, gulls, and terns) (e.g., Bildstein et al. 1982, Hicklin 1987). At many sites avian populations increase considerably, not only during migratory periods, when large numbers of waterfowl and shorebirds congregate to feed and rest in such areas, but also during the breeding season, when wading birds congregate at traditional coastal-colony nesting sites. Consequently, many coastal wetlands in the Western Hemisphere annually host significant (sensu the Ramsar Convention) portions of the world populations of a number of species (Myers et al. 1987).

For example, more than half of the Mississippi Flyway population of migratory waterfowl concentrates in wetlands along the U.S. portion of the Gulf of Mexico each winter (Southworth 1989). Between 42 and 74% of all Semipalmated Sandpipers (*Calidris pusilla*) stop to feed at a few sites along the Bay of Fundy in maritime Canada each fall (Hicklin 1987), and then move on to winter in coastal Suriname (Morrison and Myers 1987, Morrison and Ross 1989). Similarly, migrating and overwintering

Western Sandpipers (*C. mauri*) and Dunlins (*C. alpina*) assemble at a series of estuarine sites along the Pacific Coast each year (Morrison and Myers 1987). Twenty-six species of colonial waterbirds numbering more than 874,000 birds nest in coastal Louisiana, Alabama, and Mississippi alone (Portnoy 1977). More than 290 colonies of wading birds, some in excess of 40,000 birds each, occur along the east coast of the U.S. (Osborn and Custer 1978). Similarly, enormous assemblages of wading birds and shorebirds are reported for wetlands along the Atlantic coast of South America (Spaans and de Jong 1982, Morrison and Ross 1989).

Coastal wetlands sites can also be rich in numbers of species. In North America, for example, 25% of the 374 species of birds on the South Carolina state list (Post and Gauthreaux 1989) are reported from a single 3000-ha salt-marsh in the state (Bildstein et al. 1982). And in Trinidad, 39% of the 400 species of birds reported for the 4828-km^2 island have been sighted at a single 5600-ha coastal mangrove swamp (ffrench 1978, 1980).

THE POTENTIAL EFFECT OF SEA LEVEL RISE ON NESTING COASTAL-WETLAND AVIFAUNA

Although meteorologists have been hesitant to ascribe causes to global warming (Jones and Wigley 1990), a wide range of climate models have established that global temperatures have been rising over the last 100 years (Kuo et al. 1990). As a consequence, sea levels may rise by as much as 5 mm yr^{-1} (or approximately 0.3 m by the year 2050), as opposed to current increases of about 2 mm yr^{-1} (Meier 1990, but see Titus [1988: 8] for more conservative estimates). Many coastal birds nest on the ground or in floating wrack, where their nests, eggs, and nestlings are often flooded (McNicholl 1985). Rising sea levels are likely to result in more frequent flooding and possibly the complete loss of habitat for some of these birds.

Numerous factors determine the effect of high water levels on the reproductive success of coastal birds. Some are extrinsic and depend on the resiliency of the habitats to rising water levels; others are intrinsic and depend on life history characteristics of the birds.

Extrinsic Factors

Beaches and dunes.—Beaches and dunes differ in their resiliencies to rising water levels. Beaches are formed by the accumulation of sands from wave action (Smith 1990). Higher water levels will cut away beaches, leaving only high-dune vegetation. High waves, which are predicted to accompany global warming, will flatten dunes and result in fewer beaches. Most likely, new beaches will form in developed areas, where attempts will be made to restrain waves with breakwaters and other means. Hence,

the amount of beach habitat will almost certainly decline. As artificial barriers are notoriously ineffective, human development will eventually be forced inland, and eventually, beach areas should return through natural processes. Whether birds will colonize those areas will depend on the sustained availability of source populations.

Some barrier islands may migrate landward as sea levels rise. However, others will probably break up and disintegrate (cf. Titus 1988). Beach nesters using such sites (e.g., Royal Terns [*Sterna maxima*], Black Skimmers [*Rynchops niger*], Piping Plovers [*Charadrius melodus*], and Wilson's Plovers [*C. wilsonia*]) may decrease in numbers.

Salt marshes.—Salt marshes are complex ecosystems that depend on the accumulation of organic matter and mineral deposits for their formation (Smith 1990). Low-marsh vegetation, such as salt-marsh cordgrass (*Spartina alterniflora*), is well adapted to living in inundated areas, and the range of this habitat type may extend gradually inland, but only if acceleration in sea level rise is slight. Should the rate of sea level rise exceed that at which cordgrass marshes can accrete sediment and grow upward (i.e., approximately 4–6 mm/yr), substantial losses of this habitat type will occur (Titus 1988). High-marsh vegetation such as salt-marsh hay (*Spartina patens*), spikegrass (*Distichlis spicata*), and salt-marsh shrubs (e.g., *Iva frutescens* and *Baccharis halimifolia*), which is less tolerant of saltwater intrusion, is even more likely to decline. Thus, while populations of birds nesting on cordgrass or detrital wrack (e.g., Clapper Rails [*Rallus longirostris*], Laughing Gulls [*Larus atricilla*], Common Terns [*Sterna hirundo*], Forster's Terns [*S. forsteri*], Black Skimmers, Willets [*Catoptrophorus semipalmatus*]), may remain stable, or decrease only slightly; those of many wading birds nesting in high-marsh vegetation (e.g., some, but not all populations of herons, egrets, and ibises), are more likely to be reduced.

Weather.—Several models suggest more extreme weather patterns, including an increase in the number and severity of coastal storms, typhoons, and hurricanes (Emanuel 1987, Overpeck et al. 1990). Along the east coast of North America, the impact of high spring tides (those most frequently inundating nest sites) is greatly dampened by strong westerly winds that blow water from nest areas, and is intensified by strong easterly winds that blow water toward and over nesting areas. If land temperatures continue to rise, coastal areas can expect stronger onshore winds, which will exacerbate flooding problems for species nesting in either salt marshes or near the high-tide line on beaches (Meier 1990).

Intrinsic Factors

Site-fidelity patterns.—At least some coastal nesters are extremely site tenacious (e.g., Clapper Rail, Meanley 1985; Wilson's Plover, Bergstrom

1988; American Oystercatcher [*Haematopus palliatus*], Nol 1985; Willet, Howe 1982; and; possibly, Royal Tern), while others are not (e.g., Forster's and Common terns, Erwin et al. 1981; Black Skimmer, Erwin et al. 1981, Burger, 1982). Some species are facultative (e.g., Piping Plover, Haig and Oring 1988; Least Tern, Burger 1984, Kotliar and Burger 1986, Atwood and Massey 1988; White Ibis, Frederick 1987). Site fidelity should be inversely related to variance in reproductive success, which is probably related to habitat stability (McNicholl 1975). If site fidelity is genetically inflexible, then any change in habitat will spell disaster for a species. Thus, species already living in unstable habitats are likely to cope best with sea-level increases.

Habitat use.—Habitat selection and site tenacity are often closely linked. Even so, some species are extremely habitat specific but not site-tenacious (e.g., Piping Plovers, Haig and Oring 1988). For some birds, flexibility in the choice of nesting habitats could be the key to surviving increased water levels. Consider, for example Piping Plover and Killdeer (*C. vociferus*): the former is relatively inflexible in its choice of habitats, nesting nearly always on pebbled beaches on the ocean or large lakes. The beach must be clear of visual obstructions and the nests are often quite close to the high tide mark (Burger 1987). The endangered status of this species (Sidle 1985) is due, at least in part, to this inflexibility. By contrast, Killdeers nest in many human-altered habitats, sometimes at considerable distances from water, have a broad geographic range, and are expanding into northern Canada (Nol and Lambert 1984, E. Nol pers. obs.). Similarly, American Oystercatchers, Common Terns, and Laughing Gulls nesting in coastal New York and New Jersey, are flexible in nest-site selection, having moved onto wrack and dredge-spoil islands (Montevecchi 1978, Burger and Shisler 1980, Burger 1985, Lauro and Burger 1989), presumably in response to increasing human use of traditional nesting areas. Black Skimmers appear to show geographic variation in habitat selection (Gochfeld 1978; Burger 1982, 1985); some populations of Least Terns nest on roof-tops (Massey 1974), an advantageous habitat in a period of higher sea levels.

Longevity.—Most of the species considered here have high rates of adult survival (Hickey 1952). Some, such as the American Oystercatcher, are able to maintain stable, or even increasing populations, despite poor reproductive success, for up to four years (Nol 1989). Population models suggest that this is true only if annual survivorship is greater than 80%. Repeated annual losses due to high tides will be of greater consequence to species with lower rates of annual survival.

Timing of nesting.—Species with combined laying and incubation periods of less than 28 days (the time between successive spring-tide sets) can increase their reproductive success, but only if nests are initiated

immediately after a spring tide set. For example, American Oystercatchers lose most of their nests to high spring tides when peak laying is delayed until during or after the low neap tides that follow high spring tides by about one week. In species such as Clapper Rails, Piping Plovers, Wilson's Plovers, and Royal Terns, which have relatively long laying and incubation periods (all >30 d) (Meanley 1985, Wilcox 1959, Bergstrom 1988, Erwin et al. 1981, respectively), nests are exposed to two high spring tides, and reproductive success depends heavily on extrinsic factors such as weather. Increases in the severity and frequency of storms will narrow the window of safe nesting for these species. Indeed, the most serious impact of global warming on coastal-nesting birds will probably come from significant increases in onshore winds and storms.

Population projections.—Assuming that the projected rates of sea-level rise indicated above are correct, one tentative population model (E. Nol, unpubl. ms) predicts that numbers of American Oystercatchers, Piping Plovers, Wilson's Plovers, Least Terns, and Black Skimmers will decrease, while Clapper Rail, Laughing Gulls, and Common and Forster's terns, will remain stable or increase.

CASE STUDIES

The Florida Everglades and Associated Estuaries

Although no single case study could possibly be considered typical or representative of all of the issues involved in wetland conservation, the story of the Florida Everglades and associated estuaries illustrates the magnitude of some of the problems facing wetland habitat conservation efforts, especially in the developed Neotropics.

The Everglades is the largest wetland system in south Florida. Historically, the Everglades was a vast seasonally flooded wetland that extended from Lake Okeechobee south to the Gulf of Mexico (Fig. 3). This wetland system, which originally covered 9900 km^2, was made up of a mosaic of sawgrass (*Cladium jamaicense*) marshes, spike rush (*Eleocharis celulosa*) sloughs, and tree islands (Parker 1974). The Everglades was bordered on the east and west by the Coastal Ridge and Big Cypress swamp, respectively. Along the southern and southwestern border, the freshwater Everglades joined with a brackish mangrove-estuarine belt along the coast.

Seasonal rainfall is the dominant environmental variable driving wetland ecology in South Florida (Bancroft 1989). More than 80% of the annual rainfall ($\bar{x}$ = 1357 ± 259 [SD] mm, N = 25 years) occurs in a six-month period from mid-May through mid-November. Water levels rise in freshwater marshes during the rainy season and recede during the dry season, influencing the volume of water that flows into the estuaries.

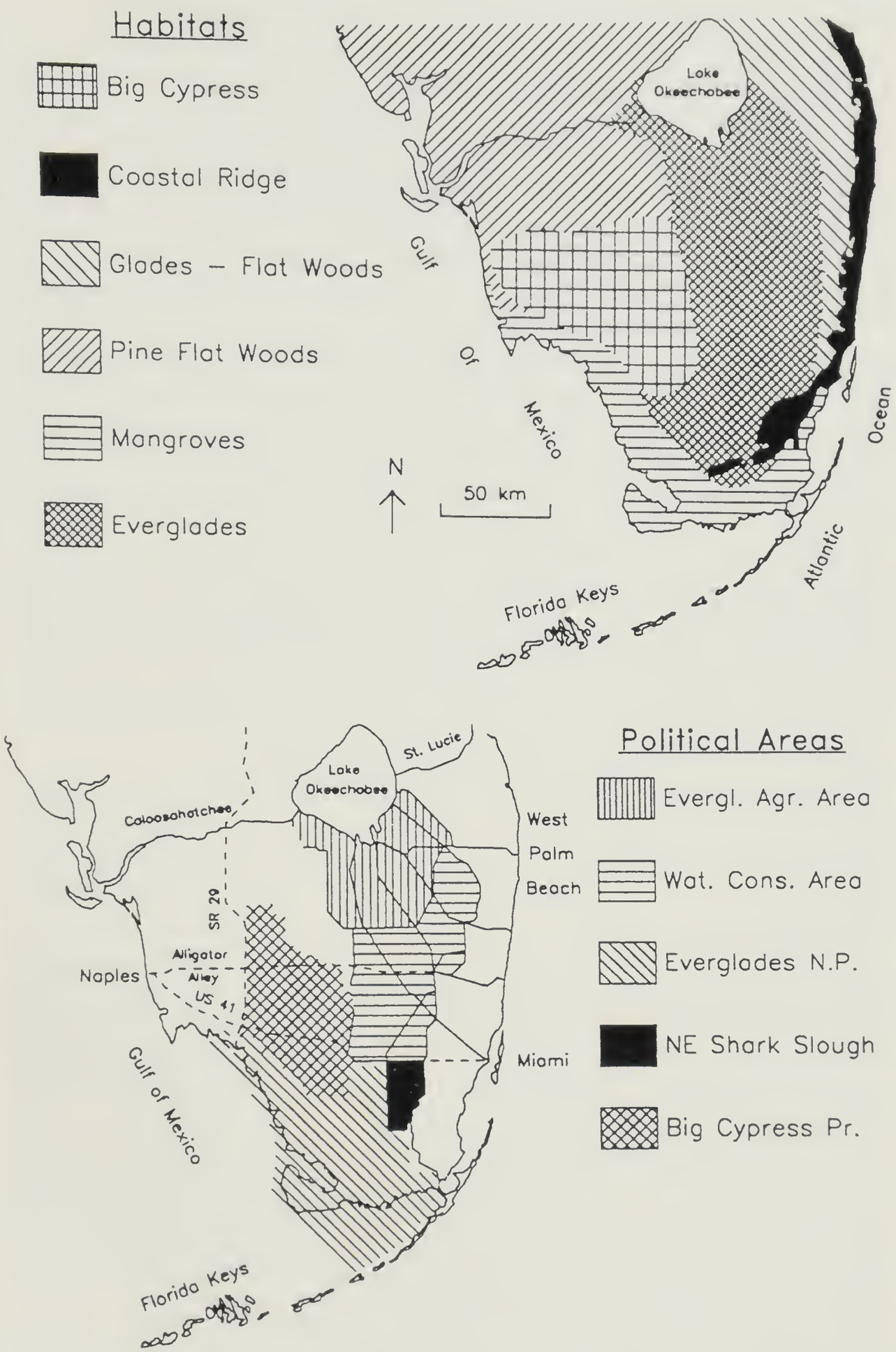

FIG. 3. The habitats of south Florida before humans began to drain the wetlands (top), and current geographic areas (bottom). Canals are shown by solid lines, roads by dashed lines.

Historically, at the height of the rainy season, the Everglades was flooded by a shallow sheet of water up to 65 km wide that flowed slowly south at less than 200 m/day (Leach et al. 1972). Water levels receded gradually during the dry season, usually reaching an annual low in May. Because of small variations in topography, isolated pools formed as water receded. These pools trapped and concentrated aquatic animals from the marshes, and large numbers of wading birds moved into the Everglades system to feed on the trapped and concentrated prey (Kushlan 1976). Wading birds nested colonially in huge numbers along the southwest edge of the system where the freshwater Everglades intertwine with coastal mangroves (Robertson and Kushlan 1974, Kushlan and Frohring 1986, Ogden 1978). Ogden (in press) estimated that, in good nesting years in the 1930s, some colonies may have contained 125,000 to 150,000 nesting pairs of wading birds.

Development of the infrastructure for water management.—The Everglades that once supported large concentrations of nesting wading birds has been modified by humans. Changes include drainage and conversion to agriculture, alteration of hydroperiods, adjustments in flow patterns, increases in nutrient and heavy-metal loading, and invasion by exotics. All of these changes have compromised the capacity of the Everglades to support large numbers of breeding wading birds.

Beginning in the late 1800s, considerable effort was invested in draining the marshes. By the early 1960s, more than 2200 km of canals and levees had been constructed (Light et al. 1989). Canals drained the northern third of the original Everglades, creating the Everglades Agricultural Area (3100 km^2; Fig. 3). The central third remains as marsh but the area is surrounded and crossed by a series of canals and levees, which form five Water Conservation Areas (WCAs) of 3400 km^2 (Fig. 3) (Tebeau 1974). Each area is managed to provide flood protection, water storage, and wildlife habitat. The southern section of the original Everglades includes Everglades National Park and an overdrained marsh east of the park known as Northeast Shark Slough (Fig. 3).

The drainage network was altered throughout the system. Flood protection for agricultural areas requires rapid removal of rainfall, resulting in unnaturally large pulses of water entering the marshes. Canals within the WCAs drain the northern sections of each area, and increase hydroperiods in southern sections of the areas.

With the completion of water control structures in 1962, water flow from the WCAs into Everglades National Park became highly regulated (Light et al. 1989). Overland flow entered the Park through four points along US highway 41, and as sheet flow across its eastern border from Northeast Shark Slough (Fig. 4). In 1967 a canal was dug along the eastern

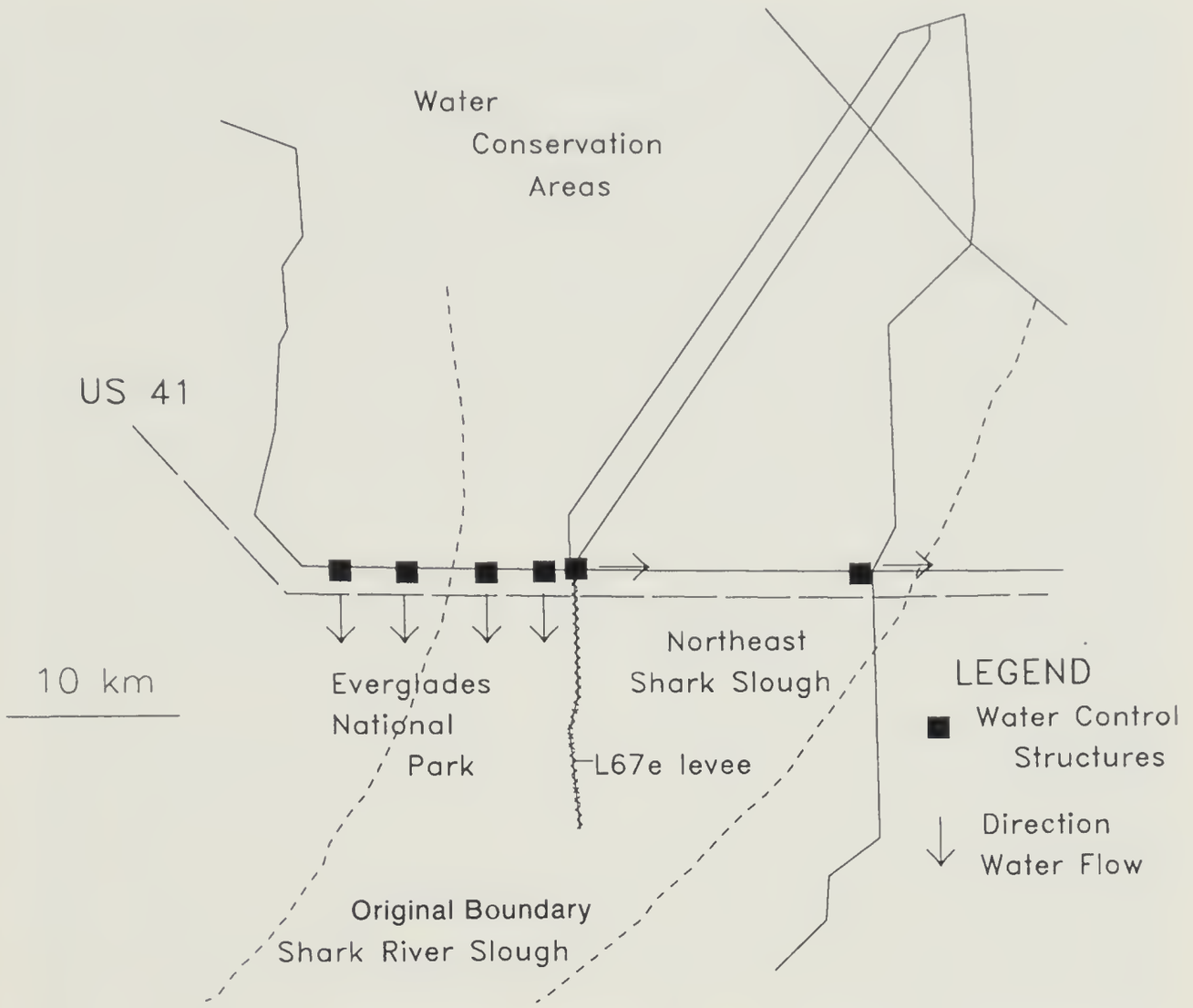

FIG. 4. Water control structures at the interface between Water Conservation Area 3 and Everglades National Park.

border of the Park immediately south of WCA 3. This canal isolated the Northeast Shark Slough, thereby changing the pattern of flow into the Park. Starting in 1962 and continuing for two years, the flow was stopped entirely. The resulting drought in the Park brought national attention to water management in the Everglades. A public outcry resulted in Federal legislation that mandated minimum monthly water delivery to the Park. This prescription, however, allowed extra regulatory releases of water to occur at the discretion of water managers.

The quality of water entering the Everglades from adjacent agricultural areas also has declined. Phosphorus and nitrogen loads are higher than occurred in the historical marsh (Davis 1989). Added nutrients have changed the periphyton community and caused a shift from a community dominated by sawgrass to one dominated by cattails (*Typha domingensis*). Both changes have decreased the value of these areas to wildlife, and in particular, their use by wading birds (Bancroft, unpubl. data). Mercury

contamination has also become a problem in the Everglades, where it accumulates in higher trophic levels and may increase mortality for top predators such as wading birds and eagles. The source of this contaminant is not known, but mercury has recently been found throughout the WCAs and the Park. One source may be naturally occurring mercury compounds found in peat soils. Peat soils are being oxidized in agricultural areas because the water table is drawn below the surface. Oxidation releases mercury, which is then washed through the system by rain.

Exotic plants and animals also threaten the restoration effort. One of the most serious exotics is cajeput (*Melaleuca quinquenervia*) which, because of its extremely high transpiration rates, was introduced into south Florida to help drain the Everglades.. This exotic, which is spreading through the Everglades, occurs in dense stands, providing poor foraging habitat for wading birds (Schomer and Drew 1982). Development of effective control measures for this plant is essential if the system is to be restored and maintained.

Effects of water management on wading birds.—Current and past water manipulations in the Everglades have resulted in decreased breeding populations of wading birds, shifts in colony sites, and a general delay in the timing of nesting. Since the 1930s, nesting populations have decreased for all species of wading birds (Bancroft 1989; Ogden, in press). More than 100,000 pairs of White Ibises (*Eudocimus albus*) attempted to nest during several years in the 1930s. During the 1970s, the maximum number attempting to nest in any year was 24,500 pairs in 1972 (Frederick and Collopy 1989). During the late 1980s, nesting efforts continued to decline, with a maximum of just over 10,000 pairs attempting to nest in 1988 (Bancroft 1989). Wood Storks (*Mycteria americana*) show similar decreases in nesting effort (Ogden and Nesbitt 1979; Ogden et al. 1987; Kushlan and Frohring 1986; Ogden, in press). The mean number of pairs attempting to nest in the 1980s was only 400, compared with 700 in the 1970s, and 1800 in the 1960s (Bancroft 1989). Nesting efforts of Great Egrets (*Casmerodius albus*), Snowy Egrets (*Egretta thula*), and Tricolored Herons (*E. tricolor*) also have decreased, although less dramatically (Bancroft 1989; Ogden, in press).

During the 1930s, most wading birds in the Everglades nested along the freshwater-mangrove interface at the southern edge of the system. Nesting birds then had the option of feeding in freshwater marshes or in brackish-water estuaries and mangroves. By the 1970s, the center of nesting for Great Egrets, Tricolored Herons, and White Ibises had shifted north out of Everglades National Park and into the Water Conservation Areas (Frederick and Collopy 1989, Bancroft 1989). Because available foraging habitat is less diverse in the Water Conservation Areas than it

is along the marsh-mangrove interface, wading birds nesting in the WCAs may be less resilient to water-level reversals caused by rainfall or water management than are birds nesting along the mangrove fringe (Bancroft et al. in press).

The onset of wading-bird colony formation has been delayed in recent decades. For example, in 14 of 16 years before 1970, Wood Storks in the Park began nesting in November and December; since 1970, storks have begun nesting after 1 January in 19 of 21 years ($G = 25.3$, df = 1, $P < 0.001$) (Ogden, in press). This temporal shift is correlated with the construction of canal L67e along the eastern border of the Park (Fig. 4) and the implementation of the minimal water delivery schedule (Ogden, in press). Few data are available for other species, but they too suggest a delay in the onset of nesting that might make it difficult for birds to complete nesting before summer rains begin. Summer rains cause water levels to rise, dispersing prey and causing problems for birds attempting to raise young (Frederick and Collopy 1989).

Recent hydrologic modeling of the Everglades strongly suggests that water management has decreased the flow of water to the estuaries (C. Walters, L. Gunderson, and C. S. Hollings, pers. comm.). Upstream water is being diverted to the Atlantic Ocean for flood protection, stored in the WCAs for later use, or used to recharge aquifers for municipal and agricultural uses. Lower freshwater flow, especially late in the dry season, may have reduced the primary productivity at the mangrove-freshwater interface (C. Walters et al., pers. comm.), which may have contributed to the major decrease in the breeding numbers of wading birds as well as to the shift in nesting locations.

Recommendations for the Everglades system.—By 1980 it was clear that water management was causing longterm degradation of the Everglades ecosystem and the modification was needed. Both the quantity and quality of water, as well as the timing of its flow, need to simulate a more natural system. Producing such patterns requires the cooperation of numerous governmental agencies.

The availability and use of water should be a major consideration in the formulation of longterm development plans for south Florida. Water rights of the Everglades need to be addressed in these plans, perhaps even mandated by the Federal government. The formulation of an overall water budget for south Florida would help define current water uses. Water conservation programs should be implemented in both urban and agricultural areas. Unlimited water should not be made available for urban areas or agriculture.

Restoration of Everglades National Park will require the redistribution of water from the Water Conservation Areas to Northeast Shark Slough

and into the Park. Congress has authorized the purchase of the Northeast Shark Slough area, and the addition of this property to the Park. Money, however, has not yet been appropriated. The levee and canal separating Northeast Shark Slough from the Park needs to be removed to allow more natural overland flow (Fig. 4). The levees and canals in the southern part of the Water Conservation Areas need to be modified structurally to allow a more natural distribution of water (Fig. 4).

Developing the appropriate management schedules for these structures will take time. Water released from the conservation areas into the Park needs to be regulated carefully, so as to simulate the natural system. The South Florida Water Management District has developed a "rainfall driven" plan to estimate the amount that should flow south. This model uses the water stored in the conservation areas plus the amount of rainfall over the previous two weeks to estimate how much water would have flowed into the park before development (MacVicar 1984). Some water from rainfall is allowed to flow south, while some is retained for storage (Walters et al., pers. comm.). This plan, which is a step in the right direction, will need to be modified as we learn more about the water budgets of south Florida and the quantities of water required in the estuaries.

Much of the land in south Florida is publicly held and, therefore, public management is at least in part responsible for maintenance of the environment. In spite of such "protection," the numbers of wading birds breeding within the Everglades system have decreased by 90% over the last 50 years. Upstream drainage and changes in the management of water flow within the natural marshes have disrupted the system. The Everglades, which will never again be total wilderness, needs to be regulated carefully if we wish to simulate the predevelopment function of this wetland.

The Arctic Coastal Plain of Alaska

Due in part to the hydrologic characteristics of permafrost, roughly half of Alaska's 155 million ha of land may be classified as wetlands. Much of that wetland acreage is coastal, including nearly all of the Arctic Coastal Plain.

The Arctic Coastal Plain includes the tundra wetlands of the North Slope and the wetlands and barrier islands of the Beaufort Sea coast, and provides valuable breeding habitats for millions of shorebirds (e.g., Semipalmated Sandpiper [*Calidris pusilla*]), waterfowl (e.g., eiders [*Somateria* spp.]), and loons (e.g., Yellow-billed Loon [*Gavia adamsii*], Derksen et al. 1981). Hundreds of thousands of postbreeding, molting, and migrating shorebirds and waterfowl (e.g., Red Phalarope [*Phalaropus fulicaria*], Snow Goose [*Chen caerulescens*]) also congregate at sites within the vast Arctic Coastal Plain (Connors et al. 1979, Garner and Reynolds 1986).

Most North Slope wetlands are intact, but subsequent to the discovery of oil in Prudhoe Bay, more than 8000 ha have been altered by the development and transportation of petroleum resources (R. G. B. Senner 1989). As virtually all of the region is legally designated as wetlands, the oil industry is chafing under the current regulatory framework, to say nothing of additional requirements that may be proposed as a result of the "no net loss" goal (see section on United States Government programs below).

In a recent report on behalf of the oil industry (ARCO Alaska and BP Exploration), R. G. B. Senner (1989) concludes that current industry practices adequately mitigate wetland losses on the North Slope and that no further regulation of wetland fills is necessary. Senner supports this conclusion "ecologically" by arguing that North Slope wetlands are less valuable than temperate wetlands and that Arctic-wetland species are not limited by habitat (i.e., wetlands are not at carrying capacity). Thus, incremental losses of wetlands do not now affect bird populations and, until population-level impacts are demonstrated, additional regulations are not justified.

In a critique of R. G. B. Senner (1989), on behalf of the Alaska Department of Fish and Game, Post (1990) reports that arctic-tundra wetlands share many characteristics with temperate wetlands, that they are reasonably productive, and that their preeminent value is as fish and wildlife habitat (Post 1990). Post concludes that migratory birds in the Arctic respond to their environment in the same way as do birds elsewhere, and that the availability of quality nesting habitats is of vital importance to avian populations.

Ultimately, issues of North Slope oil development will be resolved in political rather than technical forums. Recent political events in the Middle East have increased pressures to open areas such as the Arctic National Wildlife Refuge to oil exploration and development. This refuge is the only area on the North Slope owned by either the federal or state government that is in "protected" status. If it is developed, particularly in absence of a "no net loss" policy for wetlands (see section on U.S. Government Programs below), losses of tundra-wetland habitat due to the infrastructure (e.g., roads and gravel ponds) necessary for oil development will increase greatly.

Exploration and development of offshore sites in the Beaufort and Chukchi seas will increase the potential for oil spills in arctic marine environments, with serious implications for marine birds and wildlife in the addition to those relying on coastal wetlands. Depending on the location—for example, in the Chukchi Sea—offshore oil development also would mean additional pipelines and roadways across the North Slope feeding into the existing Trans-Alaska Pipeline, resulting in further loss

of wetland habitat. Finally, transportation of oil via the Trans-Alaska Pipeline means that more oil will leave Valdez by marine tanker. Thus, accidents similar to the one that involved the Exxon Valdez in Prince William Sound can be expected to affect coastal waters, wetlands, and associated bird populations (e.g., Piatt et al. 1990) in the future.

Central and South American Coastal Wetlands

In this section we use examples to illustrate some of the problems facing coastal wetlands in Central and South America, and discuss possible solutions to these dilemmas. Taken as a whole, our examples reflect the site-specific nature of many of these problems, and the need to consider each situation individually. Although we highlight a number of geographic regions, we offer no coverage of wetland conservation in the southern, more temperate, zone of South America, where conservation problems *and* solutions may differ from those mentioned below.

The Neotropical Realm of Central and South America, including the Caribbean Basin, is both the most biologically diverse and one of the least disturbed of the world's eight biogeographical realms. Even so, many of the region's coastal wetlands are threatened by human disturbance (Scott and Carbonell 1986, Pannier and Dickinson 1989). Caribbean wetlands appear to be the most severely threatened, while some South American wetlands, many of which are little known, appear to be the least threatened; Central American wetlands fall in between. In large part, the severity of the threat is directly related to the density of the local human population (Scott and Carbonell 1986). The ecology of many Caribbean and Latin American wetlands remains little studied, although recent publications detailing the ecology, status, and conservation of some of these wetlands (Sarmiento 1984, Scott and Carbonell 1986, Pannier and Dickinson 1989) have narrowed the gap somewhat. Here we describe several examples of the problems facing these sites, together with current and proposed management schemes that extend beyond a single-species approach.

Mangroves.—Mangroves play a crucial role in the lives of local people over much of the Pacific Coast of Central America. These forested wetlands yield timber for construction, firewood, charcoal, and tannins, and, at the same time, support productive lagoonal and offshore fisheries (Pannier and Dickinson 1989). As economic conditions in the region have declined, many individuals have lost employment, and families have had to turn increasingly to natural ecosystems to find food and income. With the decline of the banana industry in southern Costa Rica, for example, many wage earners have begun to exploit mangrove resources, either through fishing or by harvesting mangrove for the production of charcoal and the extraction of tannins. In the absence of careful management, this

rising pressure upon the resource is likely to lead to overexploitation and the gradual degradation of the resources upon which these people now depend.

In the face of this pressure, conservation efforts in several countries, most notably Costa Rica and Nicaragua, are turning away from strict protection and towards working with local people to assist them in the development and implementation of management activities that will enhance the sustainable use of the mangrove resource. In many cases where current use is not sustainable, programs are exploring ways to diversify the rural economy to increase income from other sources, thus reducing pressure on coastal wetlands. This approach not only meets rural development objectives, but, by reducing pressure on mangroves while simultaneously increasing support for mangrove conservation and management, also reduces the threat to these ecosystems posed by the growth of intensive agriculture, aquaculture, and industry.

Pesticide contamination in Nicaragua.—Pesticide levels in coastal wetlands along the Pacific Coast of Nicaragua are among the highest recorded in natural environments. Most pesticides are sprayed on cotton, which is grown along the coast. Although the use of DDT has been banned in Nicaragua since the early 1980s, many other toxic pesticides continue to be used.

Although current levels of contamination are primarily a cause of concern for public health, they also have longterm impacts on waterbird populations using these ecosystems. Accordingly, conservation efforts for Nicaragua's coastal wetlands must address not only the management of such sites, but also the broader issues of agricultural land use in the catchment. In the absence of this broader perspective, protected wetlands are likely to be seriously contaminated in the long term.

Saltwater intrusion in Trinidad's Caroni Swamp.—The Caroni Swamp is a 5611-ha mangrove-dominated coastal wetland in northwestern Trinidad, about 3.5 km southeast of the capital city of Port-of-Spain (Fig. 2). Although four rivers are associated with the estuary, most of the freshwater draining into the wetland comes from the Caroni River catchment of over 675 km^2. At least 157 of Trinidad's 400 species of birds use the swamp, including 18 species of wading birds, 14 of which reach their highest island populations there. Unfortunately, the Scarlet Ibis (*Eudocimus ruber*), Trinidad's national bird, a species that once bred in that country only in the Caroni, no longer does so. Ibises continue to feed and roost in the swamp outside of the breeding season, but during the breeding season, most adult ibises leave the island, presumably to nest in coastal South America (Bildstein 1990).

Numerous causes have been suggested for the cessation of Scarlet Ibis nesting at the site, but until recently none has been linked directly to the

consistent lack of breeding dating from 1970. Freshwater wetland losses at the site have been extensive. Seasonally flooded wetlands east of the site have been drained for housing and rice production, and the Caroni River has been channelized and diked to reduce rainy-season overflow. A four-lane, interstate-grade highway acts as a dam to freshwater surface flow into the swamp. As a result, most of the freshwater wetlands within the site are now brackish, and formerly freshwater herbaceous portions of the swamp are now dominated by mangrove forest (Bildstein 1990).

Studies of the breeding ecology of the closely related White Ibis in coastal North America suggest a link between saltwater intrusion and the cessation of Scarlet Ibis breeding activity in the Caroni Swamp. During the breeding season, parental White Ibises switch from feeding in coastal marshes on brackish-water prey to feeding almost exclusively on freshwater prey, even when this involves traveling great distances inland to do so (Bildstein et al. 1990). Experiments with hand-reared nestlings demonstrate that the dietary shift results from a physiological bottleneck in nestlings that precludes their normal growth and development on high-salt diets (Johnston and Bildstein 1990). Historical observations in Trinidad of Scarlet Ibises shifting to feed on freshwater prey during the breeding season (ffrench and Haverschmidt 1970) support the link between saltwater intrusion and a lack of breeding activity in the Caroni Swamp.

Many conservationists have called for the protection or sustainable development of mangrove swamps in coastal Central and South America. Mangrove swamps, however, are open systems and, as the above example of saltwater intrusion suggests, their protection alone will not ensure the ecological integrity of such sites. Therefore, we suggest that agencies involved in coastal-zone management consider not only coastal mangrove swamps, but also adjacent freshwater wetlands in their attempts to maintain such resources for sustainable use.

Mexico's Usumacinta-Grijalva delta.—This nearly pristine 10 million-ha wetland in Mexico's Gulf Coast states of Tabasco and Campeche, has been likened to the Mississippi River delta prior to its human modification. The delta, which is the site of the country's largest mangrove forest (currently estimated at approximately 110,000 ha), supports Mexico's highest populations of breeding colonial waterbirds, including the largest Wood Stork colony in North America. The Usumacinta-Grijalva is also the last stronghold for Mexico's dwindling population of Jabiru Storks (*Jabiru mycteria*). The Mexican government is currently considering establishing a 290,000-ha Biosphere Reserve in the Tabasco portion of the wetland. Unfortunately, PEMEX, Mexico's national petroleum company, has recently discovered high-grade crude oil at the site, threatening the site with development for its energy resources. In addition, portions of

the Usumacinta-Grijalva wetland are being modified for both rice and cattle production. This, together with recent road construction and the erection of several dams on the Usumacinta River have substantially altered the hydrology of the wetland. Indigenous inhabitants appear to be using the wetland in a sustainable fashion (e.g., the country's largest shrimp fishery is found at the site). Whether the site will be maintained intact as a functioning unit will, to a great extent, depend upon the resolve of the Mexican Government to carry through on its promised designation of the site as a UNESCO Biosphere Reserve (Rude 1989).

Coastal-zone planning in Brazil.—During the 1980s, national concern for Brazil's coastal ecosystems has grown almost as rapidly as has international concern for the Amazon. Stretching some 7500 km, the Brazilian coast contains numerous estuaries and lagoons that for centuries have played a critical role in the economy of the country. Today, however, the population of three major Brazilian cities alone (Sao Paulo, Rio de Janeiro, and Belo Horizonte) totals 30 million people. Growing population pressure in the coastal zone, coupled with a rising demand for economic growth, has resulted in the severe degradation of many coastal ecosystems. Populations of fishes, shrimps, oysters, and crabs are dangerously contaminated with mercury and other heavy metals, while demand for agricultural land is leading to reclamation of coastal land and diversion of freshwater from many estuarine systems, thus reducing their productivity (cf. Neves 1989).

In response to development pressure, there is now increasing awareness of the importance of coastal wetlands and the need for urgent action to ensure that these systems will continue to yield a diversity of benefits. In 1988 the Brazilian government enacted a National Coastal Zone Management Plan (PNGC), and a number of governmental and nongovernmental projects are now underway along the coast, including the "macrozoning" of the region based on information organized in 30′ by 30′ geographical sections (Frischeisen et al. 1989). Twelve classes of coastal types have been established, including Ecological Conservation Areas, Scientific Research Areas, Ports and Terminals, Urban Expansion, Farming Activities, Aquaculture Activities, etc. Ecological Conservation Areas, for example, include portions of the Mata Atlantica, a coastal-zone tropical rain forest, which would be preserved in an attempt to maintain the natural hydrological cycle of the region, as well as the deltas of most major rivers, and mangroves (Azevedo et al. 1989).

To be successful, conservation efforts need to go beyond management of individual estuaries and address broader issues related to the distribution, form, and intensity of all economic activities in the coastal zone. This will require extensive consultation at local, state, and federal levels,

a task that has been greatly facilitated by the establishment of the International Commission for Marine Resources, which has provided leadership and guidance to work undertaken by individual states.

An example of the type of initiative supported by the Commission is a conservation program for the Iguape-Cananeia-Paragua estuary system in Sao Paulo and Parena states. A coastal-zone management plan that identifies the most promising management options and economic investment has been developed for the estuaries and surrounding basins. In preparing the plan, conflicting issues were resolved by a coastal committee of representatives of government institutions, fishermen and peasant associations, entrepreneurs, and environmental groups.

Along with the management plan, the program has taken steps to improve the living conditions of the people and to encourage their cooperation with conservation actions. Improvements include support to oyster farming, subsidizing transport of farm products and fish and oysters, and helping to establish a facility for fish-smoking. Because smoked fish can be transported more easily than fresh fish, and therefore are more valuable, the program increases local income without increasing demand on the resource.

Conclusions.—The message from these Caribbean and Latin American examples is clear. The conservation of coastal wetlands is a complex process, which today reaches far beyond the traditional, wildlife-oriented approach of simple wetland preservation. Only by considering the full range of issues, including the biological importance of the resources, the uses made of these resources by local inhabitants and their importance to the local economy, external threats from pollution and water diversion, and the administrative structures at the local and national level that will oversee and implement management, can longterm success be achieved.

INTERNATIONAL PROGRAMS

Here we provide information on two international programs, the Western Hemisphere Shorebird Reserve Network (WHSRN) and the North American Waterfowl Management Plan (NAWMP), both of which are involved in coastal wetland conservation in the Western Hemisphere. Although not described herein, several other international groups, including the International Waterfowl and Wetlands Research Bureau (IWRB; Slimbridge, England) and the International Union for the Conservation of Nature and Natural Resources (IUCN; Gland, Switzerland), are also actively engaged in the conservation of coastal wetlands in the New World. IWRB, for example, has just published the results of a symposium on Scarlet Ibis conservation (Frederick et al. 1990), and is currently cooperating with WHSRN in a joint census of Neotropical shore-

birds and waterfowl. IUCN, on the other hand, is currently preparing a document that will focus on the sustainable development and wise use of the world's wetland resources.

The Western Hemisphere Shorebird Reserve Network.—WHSRN was launched in 1985 in response to declining shorebird populations and disappearing wetlands. Initial collaborating groups included the International Association of Fish and Wildlife Agencies, the World Wildlife Fund, and the Academy of Natural Sciences of Philadelphia, the Canadian Wildlife Service, National Audubon Society, and Manomet Bird Observatory (Myers et al. 1987). The network brings together wildlife agencies, land owners, private conservation groups, and others to solve conservation challenges faced by migrating shorebirds and the wetlands they use. Membership and participation in WHSRN is voluntary; management authority and priorities remain the prerogative of the land administrator. The Network's success ultimately depends upon the involvement of enthusiastic people in wildlife agencies, park systems, governments, and private groups that own and manage wetlands.

WHSRN is compatible with and encourages participation in other national or international conservation programs, and supports a variety of conservation approaches, including sustainable development and critical management. Several WHSRN sites are wetlands protected under the Ramsar Convention. The U.S. Fish and Wildlife Service has nominated a number of National Wildlife Refuges for inclusion in the system, as has the Suriname Forest Service.

To be included in the network, a site must meet certain biological criteria. Hemispheric Reserves are used by at least 500,000 shorebirds annually or 30% of a flyway population. International Reserves host at least 100,000 shorebirds annually or 15% of the flyway population. Regional Reserves host 20,000 shorebirds annually or 5% of the flyway population. Endangered Species Reserves are of critical importance to the survival of an endangered shorebird species; no minimum number of birds is required. Pairing or "twinning" of sites that share high numbers of the same species at different points in the hemisphere reinforces cooperation on a hemisphere level and facilitates exchange of scientific data. As of the spring of 1991, 11 Hemispheric and three International reserves have been included in the Network, with many others waiting in the wings. Reserves include Delaware Bay, USA; Bay of Fundy, Canada; Wia-Wia, Coppename, and Bigi Pan, Suriname; Stillwater NWR, USA; San Francisco Bay, USA; Cheyenne Bottoms, USA; Laguna Mar Chiquita, Argentina; Copper River Delta, USA; Maryland-Virginia Barrier Islands; Lagoa do Peixe, Brazil; and Mono Lake, USA. Sites in Canada's Bay of Fundy and coastal Suriname have been "twinned." The establishment of the Stillwater site

has led Congress and the Federal government to take the precedent-setting step of buying water rights for wildlife refuges.

WHSRN works cooperatively on many levels to increase research and management efforts to benefit shorebirds and wetlands. In the neotropics WHSRN co-sponsors workshops for biologists and policy makers. Field workshops offer participants the opportunity to develop biological skills necessary for gathering data on wetlands and shorebirds. Policy-management workshops offer management information and discussions of current and proposed management plans. As of spring 1991, workshops have occurred in Argentina, Chile, Brazil, Ecuador, Mexico, Peru, and Venezuela. In North America WHSRN works with multiagency efforts such as the North American Waterfowl Management Plan to increase management possibilities for shorebirds and other nogame wetland species at some joint ventures.

The Network operates through a representative council and staff. The former establishes policy, offers guidance, and stimulates development of the Network. The latter works to bring new sites into the Network, provide management guidelines, research information, and educational materials to existing sites, coordinate neotropical workshops, manage data bases, and inform the public. The Network's philosophy is to build on existing resources and to unify local and regional groups, rather than to import expertise. Additional information about the program is available from WHSRN, Manomet Bird Observatory, Manomet, Massachusetts 02345, USA.

The North American Waterfowl Management Plan.—Recognizing the need to reverse precipitous declines in North American waterfowl populations and the continent-wide destruction of wetland habitats, in 1986, representatives of the United States and Canada co-signed an historic document called the North American Waterfowl Management Plan (NAWMP). NAWMP is an international strategy that provides a cooperative framework for waterfowl conservation and management efforts between the two countries through the year 2000. The program is designed to promote the longterm perpetuation of North American waterfowl populations through the protection, restoration, and management of an appropriate distribution and diversity of high quality waterfowl habitat across North America (Fig. 5).

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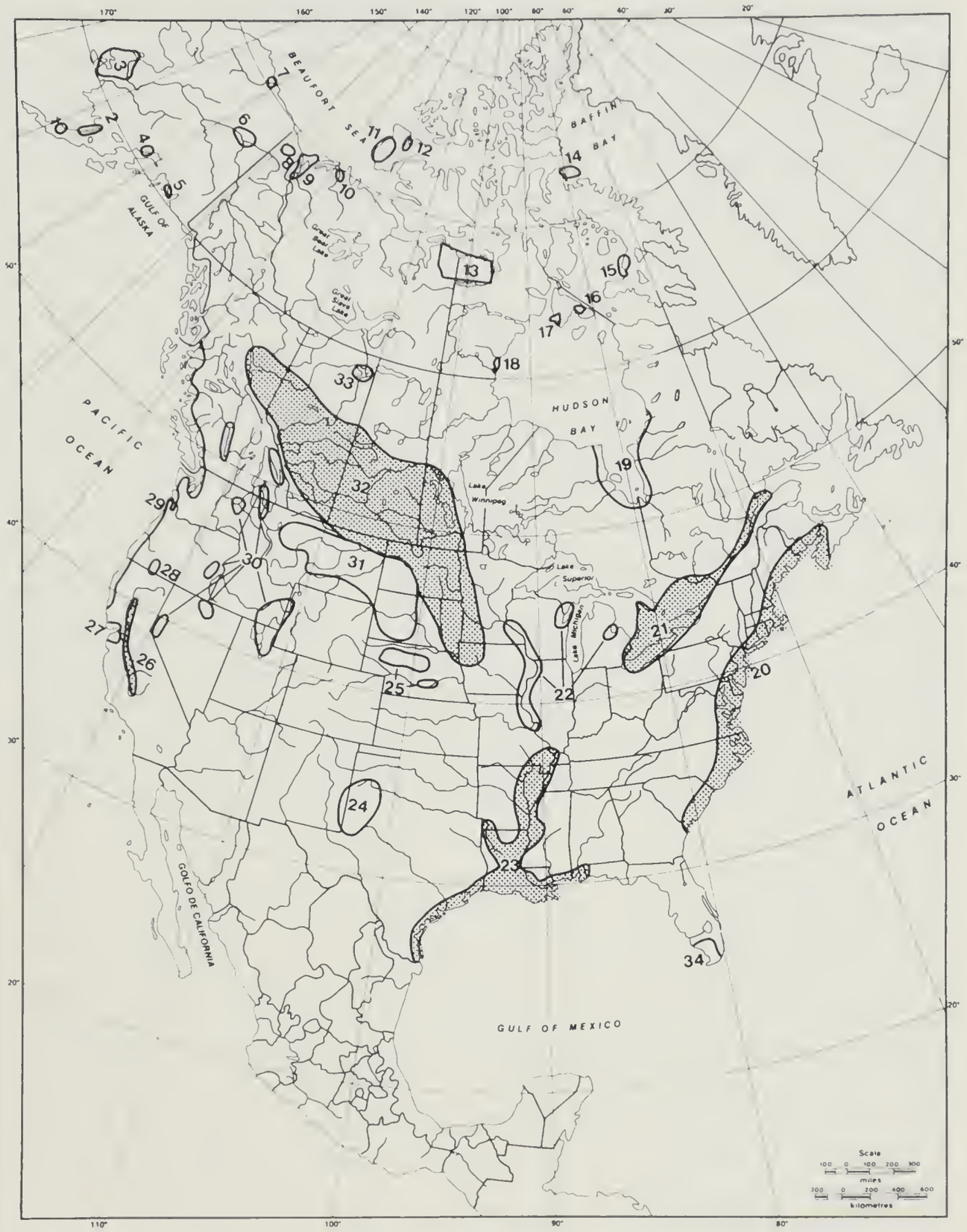
FIG. 5. Waterfowl habitat areas of major concern in the United States and Canada (1, Izembek Lagoon; 2, Upper Alaska Peninsula; 3, Yukon-Kuskokwim Delta; 4, Upper Cook Inlet; 5, Copper River Delta; 6, Yukon Flats; 7, Teshepuk Flats; 8, Old Crow Flats; 9, Mackenzie River Delta; 10, Anderson River Delta; 11 and 12 Banks Island, 13, Queen



Maud Gulf; 14, Bylot Island; 15, Dewey Soper; 16, East Bay; 17, Harry Gibbons; 18, McConnell River; 19, James Bay Lowlands; 20, Middle-Upper Atlantic Coast; 21, Lower Great lakes-St. Lawrence Basin; 22, Upper Mississippi River and Northern Lakes; 23, Lower Mississippi River Delta and Gulf Coast; 24, Playa Lakes; 25, Sandhills and Rainwater Basin; 26, Central Valley; 27, San Francisco Bay; 28, Klamath Basin; 29, Middle-Upper Pacific Coast; 30, Intermountain West; 31, Northern Great Plains; 32, Prairie Potholes and Parklands; 33, Peace-Athabasca Delta; 34, Southern Florida). (A similar map appears in publications of the North American Waterfowl Management Plan.)

NAWMP has set population goals for 32 species of ducks, geese, and swans; has identified habitat conservation needs and goals (in excess of 2,400,000 ha) for specific regions of the continent and provided an international plan of action to achieve these goals. Because the loss and degradation of habitat is perceived as the major problem facing waterfowl management in North America, NAWMP emphasizes that the continued maintenance and restoration of wetlands is necessary to provide suitable habitat for waterfowl and many other wetland-dependent species.

The Plan's ambitious goals, large geographic scope, and projected costs in excess of $1.5 billion mean that its successful implementation will occur only with the participation and close cooperation of both public and private organizations in the U.S. and Canada. This has been accomplished through the membership of the Plan's three standing governing bodies. The 12 member North American Waterfowl Management Plan Committee includes representatives of the U.S. Fish and Wildlife Service, the four flyway councils, the Canadian Wildlife Service, and the Canadian provinces and territories. NAWMP Implementation Boards for the U.S. and Canada, operating under this committee, include representatives from Ducks Unlimited, Inc., Ducks Unlimited Canada, the National Fish and Wildlife Foundation, The Nature Conservancy, the National Audubon Society, Wildlife Habitat Canada, the American Farmland Trust, WHSRN, and the American Forest Foundation, among others. Together, these three groups oversee the development, coordination, funding, and review of NAWMP activities.

In addition to the above continental committees, regional Joint Ventures that are coalitions of state and federal agencies, conservation groups, and individuals have been established for key habitat priority areas. The six Joint Ventures in the United States are the Atlantic Coast, Lower Great Lakes-St. Lawrence Basin, Lower Mississippi Valley, Prairie Pothole Region, Gulf Coast, and Central Valley of California. Detailed Joint Venture Plans identify regional goals and objectives for restoring waterfowl populations and wetland habitats. Partners in each Joint Venture combine their collective resources and cooperate in planning, funding, and implementing projects.

Funding for NAWMP comes from many sources. Initially, money was generated through an innovative challenge-grant program in which $1,000,000 contributed by 12 state fish and wildlife agencies was matched by Ducks Unlimited. This amount was matched again by the National Fish and Wildlife Foundation and Canadian government, resulting in an $8,000,000 program, which has been spent primarily on the Prairie Habitat Joint Venture in Canada. As NAWMP has become a reality and garnered additional support, substantial funds are being directed to NAWMP Joint Venture activities by participating government agencies,

conservation groups, and private individuals. The North American Wetlands Conservation Act (see below) will provide a significant source of federal funds for NAWMP wetland conservation projects.

Many creative strategies are being used to meet the goals and objectives of NAWMP Joint Ventures, including fee-title land acquisitions; restrictive conservation easements; cooperative agreements among corporations, public agencies, and private landowners; leases; financial incentives; technical assistance; and information and education programs, all of which are being successfully used to protect and enhance key wetland and associated upland habitats. Efforts are also underway through NAWMP to improve government regulatory and assistance programs that impact wetlands acquisition, restoration, management, and enhancement activities, and to improve existing federal agency land acquisition and management programs.

NAWMP will play an important role in the conservation of coastal wetland ecosystems important to waterfowl and other wetland-dependent species. Both the Atlantic Coast and Gulf Coast Joint Ventures focus on major coastal wetland regions of the United States. Projects in both joint ventures are already underway to protect key wetlands from further loss and degradation due to impacts from residential and commercial development, industry, navigation, agriculture, and intensifying recreational use. Many of these projects have been designed to encompass large-scale coastal upland-wetland complexes with the intent of protecting and enhancing functional wetland ecosystems that benefit the most species. The ACE Basin Project in South Carolina, the Cape May Project in New Jersey, and the Milford Neck Project in Delaware are good examples of this aspect of NAWMP.

The 140,000-ha Ashepoo, Combahee, and Edisto (ACE) Rivers Basin is one of the largest remaining undeveloped coastal wetland ecosystems along the U.S. Atlantic Coast. The basin encompasses several undeveloped barrier islands; approximately 37,000 ha of tidal marsh, including 26,000 acres of salt marsh, 5500 ha of brackish marshes, and 4900 ha of freshwater marshes; and over 22,000 ha of forested wetlands. Approximately 10,500 ha of managed wetland impoundments are interspersed within the three tidal zones. This diverse complex of wetland communities and associated uplands performs many important functions and has great value as a natural resource.

The ACE Basin has been identified as a unique coastal wetland ecosystem of national and regional significance through the criteria of the National Wetlands Priority Conservation Plan (Emergency Wetlands Resources Act of 1986) and has been listed as a target for preservation in the Draft Southeast Regional Wetlands Concept Plan. The basin's value to wildlife and the overall ecological significance of the area as a largely

intact coastal wetland system have spawned a major initiative to preserve the area in perpetuity.

Identified as a flagship project of the NAWMP Atlantic Coast Joint Venture, the ACE Basin Project exemplifies NAWMP efforts to protect entire coastal wetland systems. The project is comprehensive in scope, with the overall objective being to protect, enhance, restore, and manage an appropriate distribution and diversity of wetlands and associated uplands for migratory birds and other wildlife. Consideration is given to threatened and endangered species (e.g., Bald Eagle [*Haliaeetus leucocephalus*], Wood Stork), estuarine fisheries, and unique and valuable plant communities.

Planning and implementation of the ACE Basin Project is being coordinated through the cooperative efforts of Ducks Unlimited, Inc., the South Carolina Wildlife and Marine Resources Department, the U.S. Fish and Wildlife Service, The Nature Conservancy, the National Fish and Wildlife Foundation, and many private landowners. Together, these partners have developed an innovative strategy to preserve the ACE Basin using voluntary conservation easements by private landowners and public and private land acquisitions. Presently, over 4800 ha of brackish and freshwater wetlands are protected within a state wildlife management area. The U.S. Fish and Wildlife Service is proceeding with the establishment of a 7300-ha National Wildlife Refuge, and another 6500 ha will be protected within a National Estuarine Research Reserve (see below). The Nature Conservancy is working with private landowners to protect additional wetlands and adjacent uplands through conservation easements. Ducks Unlimited is coordinating protection strategies involving easements and fee acquisitions for other parcels of property key to maintaining the ecological integrity of the basin's wetland ecosystem. All aforementioned cooperators have provided funds to support Project activities, and additional funding from the North American Wetlands Conservation Act is anticipated.

UNITED STATES GOVERNMENT PROGRAMS

Many segments of the U.S. government are involved in wetland conservation. Here, we describe recent actions of the Executive and Legislative branches, together with those of a number of key agencies, including the U.S. Fish and Wildlife Service (FWS), the National Park Service (NPS), the Environmental Protection Agency (EPA), the National Oceanic and Atmospheric Administration (NOAA), and the U.S. Army Corps of Engineers (COE).

The Executive Branch.—President Bush has taken an active posture in declaring that there will be "no net loss" of wetlands in the U.S. This

declaration was a response to the recommendations of the National Wetlands Policy Forum report (The Conservation Foundation 1988), which can be summarized as follows.

First, an emphasis is placed on protecting wetlands by reducing losses and increasing restoration efforts. Second, efforts are to be aimed at improving protection and management processes through regulatory programs and education. Third, implementation of the Forum's recommended program requires that Congress enact legislation that will establish wetland protection goals as national policy, that qualified states be granted stronger wetlands regulatory responsibilities, that incentives such as Wetland Preservation Trusts and an Agricultural Wetlands Reserve Program be established, and that the President be required to report to Congress every five years on progress on national wetlands goals.

Parts of the Forum report have been controversial (Wood 1990). There is some debate over the relative roles of states and the Federal government in wetland permit administration and protection. Major differences exist in the level of state protection of wetlands across the U.S.

President Bush appointed a Domestic Policy Council to develop an interagency document to guide future Federal actions. This council has to deal with competing interests of conservation, land development, and oil and gas leases. Progress has proved to be slow because of conflicts over energy development and transportation in Alaska and preoccupation with the Clean Air Act.

U.S. Fish and Wildlife Service.—The FWS has planned or recently initiated a number of important ventures that bear directly on wetland conservation. The North American Waterfowl Management Plan (described above) has received a major boost with the passage of the North American Wetlands Conservation Act.

In response to the President's call for "no net loss" of wetlands, the FWS has developed a step-down plan for a wetlands initiative, "Wetlands: Meeting the President's Challenge." This document (still under review in the Department of the Interior) takes a three-prong approach to "no net loss." First, it focuses on reducing and trying to eliminate the rate of loss, using the regulatory process, easement or lease programs, review of Federal projects, and cooperative efforts with other agencies and with public and private organizations. Second, wetland restoration, enhancement, and management will be emphasized. Greater effort will be expended, both on National Wildlife Refuges and other public and private lands, to benefit waterfowl and other wildlife, including endangered species. Wetlands creation, because of the many technical problems, remains a tool with limited application at present. Third, a stronger thrust will be directed at wetlands research, information transfer, and education. Research will be directed

at wetland functioning at the community and ecosystems levels. Education and research will be expanded in the hemisphere under the Ramsar Convention.

Under the umbrella of the Wetlands Initiative, the FWS has formed a Coastal-Estuary Working Group. The draft report of that group recommends that the Director improve coordination with other agencies, especially EPA, NOAA, and COE. It reiterates many of the same research, management, and education goals of the Initiative, but calls for a stronger research thrust into wetlands functioning. It also recommends the removal of economic subsidies for coastal development, such as was done through passage of the Coastal Barrier Resources Act in 1982 (see below). It suggests that a FWS national coastal and estuary program be established. There already exists a Chesapeake Bay Estuary Program, as well as new programs began in 1989 in Delaware Bay, in southern New England, and on Long Island Sound. Plans are being made to expand to Galveston Bay and, later Puget Sound.

The FWS National Wetland Inventory has produced detailed 1:24,000-scale wetland maps for the entire coastal zone of the conterminous United States, Hawaii, and the Great Lakes. Maps are available by calling 1-800-USA-Maps (in Virginia, [703] 648-6045).

National Park Service.—The NPS has been embroiled in recent controversy over its policies on National Seashores concerning offroad vehicle permits on beaches, dunes, and associated wetlands. Legal decisions on Cape Cod National Seashore have supported the agency's ability to uphold restrictions for the protection of the endangered Piping Plover and other beach-dependent species. However, recreational versus conservation conflicts remain at Fire Island, Cape Hatteras, Assateague, and other National Seashores. Although beaches, arguably, may not be considered wetlands, disturbances from vehicular traffic on outer beaches and dunes certainly have indirect effects that extend to adjacent wetland use by birds.

At Fire Island National Seashore on Long Island, New York, the NPS has also initiated wetland restoration projects in salt marshes that have been altered for mosquito control. These projects should enhance the value of these wetlands to waterbirds and shorebirds. At the NPS Jamaica Bay Refuge, also on Long Island, park personnel have been managing water levels at two impoundments for shorebirds (P. Buckley, pers. comm.).

As indicated above, the passage of the recent Everglades National Park expansion has been a major conservation victory for wetlands and wildlife. Another major confrontation has occurred with regard to water rights in the Park. Legal action is pending between the South Florida Management District and the Department of Justice concerning agricultural water uses and runoff into the Everglades. There is major concern within the conservation community that both water quantity and quality must be en-

hanced if there is to be any success in restoring wildlife and fish to the region.

National Oceanic & Atmospheric Administration (Department of Commerce).—NOAA has several programs that are relevant to wetland conservation, including:

(a) The National Estuary Inventory Program.—The intent of the program is to assimilate biological, chemical, and physical data on estuaries into a system compatible with desk-top computers. This system is intended to be used to identify water-quality problems, map important resource areas, and identify trends of resource changes over time and space. Nationwide, NOAA's program supports an inventory of 120 estuaries. Program goals show some overlap with the FWS Coastal-Estuary Program and EPA-sponsored projects in many estuaries.

(b) The National Estuarine Research Reserve Network.—This program matches Federal with state funds on a 50:50 basis to support research on 18 reserves, ranging from one to 196,000 ha. These reserves are under state protection. Twelve of the current reserves are on the Atlantic Coast, one is on the Great Lakes, one in Hawaii, and four on the West Coast. Four of the five currently under consideration are on the East Coast. The network protects important wetland habitats for birds, augmenting the lands within the National Wildlife Refuge system, National Seashores, and other public and private wildlife sanctuaries.

(c) The Coastal Ocean Program.—This new program has a large research component. It focuses on energy flows and modeling and includes ocean systems, ocean-coastal interactions, and upland-estuary coupling.

U.S. Army Corps of Engineers.—In a number of districts, the COE has become much more responsive in recent years to concerns for wetland quality, as well as quantity. With respect to bird conservation issues, there are a number of examples where dredge operators have worked cooperatively with biologists in adding fresh-dredged material to currently existing islands in attempts to enhance the habitat for nesting colonial waterbirds. A recent emphasis has been closer cooperation among regulatory personnel in COE, EPA, and FWS.

The momentum of the "no net loss" initiative was slowed by negotiations over details of a memorandum of agreement between COE and EPA. Sensitive issues had to do with the concept of "sequencing," whereby wetland loss is, first, to be avoided, second, to be minimized, and third, to be mitigated by creation or restoration. Points of contention dealt mainly with dredging operations under Section 404 guidelines of the Clean Water Act. Now that the agreement has recently been signed, progress on "no net loss" should continue through 1990.

The Environmental Protection Agency.—As indicated above, a recent hurdle has been overcome with respect to how dredge and fill operations

proceed and how final authority for permit issues is resolved. There is broad recognition at all levels of government that there is too much "red tape" involved in regulatory matters and that there is often no clear lead agency on a number of wetland issues. The EPA appears to have broadened its mission in recent years, going beyond traditional water-quality concerns in wetlands.

The EPA has launched a new initiative called the Environmental Monitoring and Assessment Program (EMAP). The initiative has implications for wetland quality and conservation because of its intent to monitor physical, chemical, and biological resource data on a national scale, using 12,500-grid sampling points. Waterbird abundance is one of seven wetland "condition" parameters being proposed for monitoring. The program, which carries a price tag of well over $100 million, is intended to integrate monitoring over all Federal resource agencies.

Legislative Branch.—Several acts have been signed into law recently that have a direct bearing on waterbird conservation in the U.S.:

(a) The Everglades National Park Protection and Expansion Act, signed in late 1989, authorizes, pending the necessary appropriations, expansion of the park by 44,350 ha on the northeastern boundary. It also bans most uses of airboats in the park.

(b) The North American Wetlands Conservation Act, also signed in late 1989, emphasizes wetlands protection for migratory birds in the U.S., Canada, and Mexico. The law highlights endangered species and migratory nongame birds as well as waterfowl. A funding base is established that taps three sources of funding: interest on investments from Pittman-Robertson funds, additional funding (up to $15 million) from Department of Interior appropriated funds, and a smaller amount from fines, penalties, and forfeitures from Migratory Bird Treaty Act violations. Matching (non-Federal) funds are to be used for all projects; proposals submitted are reviewed by a new council that makes recommendations to the Migratory Bird Commission for funding. From 50-70% of the anticipated $50 million per year is to be used for projects in Canada and Mexico.

Two other major bills are pending that also have major implications for bird conservation in wetlands:

(a) The Louisiana Coastal Wetlands Conservation and Restoration Act would develop a plan to slow the loss of state wetlands, design a permit program for development activities in wetlands with provisions for no net loss of area, and set up a fund to finance coastal restoration projects. The major sticking point so far has been the financial provision. One suggestion has been that 5% of the oil and gas lease revenues from the outer continental shelf be set aside as a trust. Work on the bill continues.

(b) The Coastal Barriers Resources Act (COBRA), pending in the House, would add 320,000 ha of Atlantic and Gulf Coast land and 23,000 ha of

coastal habitat in the Great Lakes to the existing Coastal Barrier Resources System and would map the Pacific Coast for area designations. The most current version of the bill deals only with private lands, omitting military and NPS lands under COBRA. The original legislation, which was signed in 1982, withdrew Federal subsidies for development of what were then undeveloped barrier islands on the Atlantic Coast.

As this summary indicates, many aspects of wetland conservation, management, and research are on the forefront of Federal actions, in large part as a consequence of the current pledge of "no net loss." If the recommendations of the National Wetlands Policy Forum are implemented, a great amount of Federal and state resources will need to be marshalled to ensure that wetland losses and alterations are reduced, that the regulatory process is improved, and that economic and other incentive programs are put in place to augment current Federal, state, and private wetland holdings.

SUMMARY AND RECOMMENDATIONS

Although coastal wetlands comprise less than 3% of the land surface of the Western Hemisphere, these areas include some of the most productive and ecologically valuable of all natural habitats. Approximately half of the hemisphere's human population lives near and depends on coastal wetlands which are open ecological systems that can be used by human populations in a sustainable manner. Unfortunately, many coastal wetlands continue to be altered detrimentally, both directly and indirectly, at an alarming rate by the actions of human populations throughout the hemisphere.

The committee recommends (1) that appropriate local, state, and natural governmental and nongovernmental organizations in the Western Hemisphere enhance and ensure the protection of these important ecological resources by supporting essential research, by the passage of new protective and regulatory legislation as warranted, and by the enforcement of existing laws concerning wetland use; (2) that nations that have not already done so, become contracting parties to the Convention on Wetlands of International Importance Especially as Waterfowl Habitat (the so-called RAMSAR Convention), that all nations adhere to both the spirit and letter of this international treaty, and that they actively promote the wise and sustainable use of coastal wetlands within and beyond their jurisdictions, (3) that nations create strong local and national conservation programs, and that they become involved with the Western Hemisphere Shorebird Reserve Network, the North American Waterfowl Management Plan, and other international programs fostering similar goals, (4) that nations with useful technical information provide such information to other nations so that the latter may make informed decisions concerning

the management of their coastal resources, and (5) that educational campaigns be initiated throughout the hemisphere to heighten public awareness of the plight of coastal wetlands, thereby increasing the likelihood that these valuable resources will be used wisely.

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SHORT COMMUNICATIONS

Geographic variation among Sage Grouse in Colorado.—Sage Grouse (*Centrocercus urophasianus*) occur only in the sagebrush (*Artemisia*) ecosystem of western North America. The species is entirely dependent upon sagebrush for seasonal cover and winter forage (Eng and Schladweiler 1972, Wallestad 1975, Remington and Braun 1985), and except during summer, does not occur in areas where sagebrush is absent. Geologic features, areas of unsuitable soil, and natural and human perturbations have created discontinuities in the sagebrush ecosystem. Consequently, the distribution of Sage Grouse is not continuous (Fig. 1), and some populations are separated by areas of unsuitable habitat. Morphological differences may exist among allopatric populations of Sage Grouse if areas of unsuitable habitat have created barriers to gene flow.

In Colorado, Sage Grouse occur in several montane basins. Typically, sagebrush dominates the basin floors. The surrounding mountains are dominated by subalpine or alpine vegetation that may inhibit movement of Sage Grouse. Sage Grouse wings obtained from hunters suggested that Sage Grouse in the Gunnison Basin (Gunnison and Saguache counties) in southern Colorado were smaller than grouse in other populations in the state (Braun, unpubl. data). To determine if phenotypic differences existed among allopatric populations, we compared morphological features of Sage Grouse in the Gunnison Basin to those of Sage Grouse in North Park (Jackson County) in northern Colorado. Because both populations occur within the range of *C. u. urophasianus* (Aldrich 1963), phenotypic differences could indicate that subspecific classification of Sage Grouse should be reevaluated.

Methods.—Both study areas are montane basins in which sagebrush dominates large areas (>1600 km^2) between 2300 and 2900 m in elevation (Beck 1977, Hupp and Braun 1989a). Surrounding mountains are approximately 3100 to 4200 m in elevation. The two populations are about 200 km apart, although Sage Grouse occupy other montane basins between North Park and the Gunnison Basin.

Morphological measures were obtained from two sources in each population for four categories of age and sex; adult (>21 months of age), yearling (9–11 months of age), males, and females. The first was a sample of 97 adult males collected on leks from 1984 to 1986 for analysis of body composition (Hupp and Braun 1989a). With the exception of 1986, adult males were collected in time periods that corresponded to early and late courtship in April and May, respectively. Data for other categories of sex and age were from individuals trapped, marked, and released between March and June, 1983–1985 in North Park and 1984–1985 in the Gunnison Basin. Birds were usually trapped by spotlighting on or near leks (Giesen et al. 1982).

We measured live body mass (±5 g) and body mass minus ingesta in the digestive tract of collected males. We also measured lengths of the tarsus (base of the middle toe to the proximal end of the tarsus), culmen (straight line from tip of the upper mandible to the insertion of feathers above the mandible), and carpal (wrist to tip of the longest primary with the wing slightly flattened). We recorded live body mass of females and yearling males that were captured and marked. We also measured carpal, tarsus, and culmen lengths of females and yearling males captured in the Gunnison Basin, and also obtained the same data from a small sample of yearling males collected on leks in North Park during April 1984. Carpal lengths of females and yearling males in North Park were measured in 1983.

Body mass of adult male Sage Grouse varies both seasonally and annually due to fluctuations in lipid reserves (Beck and Braun 1978, Hupp and Braun 1989b). Comparisons of body mass of adult males in different populations should be made cautiously to insure that temporal variation is not mistaken for geographic differences. We evaluated within- and

FIG. 1. Current distribution of Sage Grouse in North America (Western States Sage Grouse Comm. 1985:19).

among-year variation of morphological features of adult males. We used analysis of variance (ANOVA) to test for differences between early and late periods of courtship (nested within years and populations) for those years (1984–1985) in which birds were collected in the two time periods. Data from different collection periods were pooled within years when analyses indicated no differences. A second ANOVA assessed differences among years (1984–1986, nested within populations) and between populations.

Morphological features of female and yearling male Sage Grouse were compared between populations by Mann-Whitney tests (Conover 1980:216) due to small sample sizes in the Gunnison population. We pooled data among years because of small sample sizes and made no attempt to assess variation within or among years for females and yearling males.

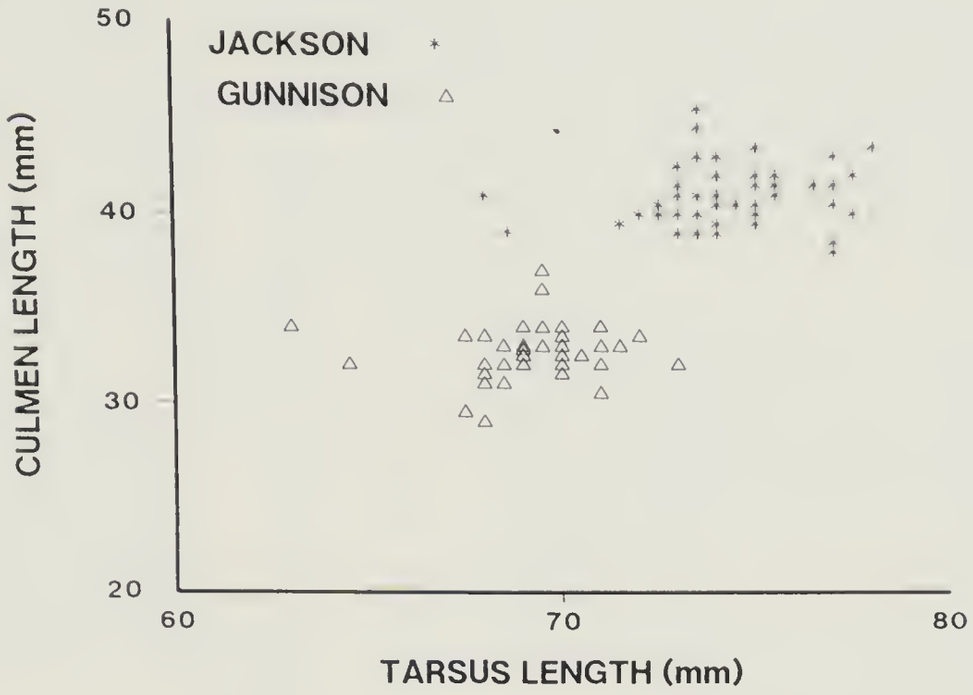

FIG. 2. Comparative tarsus and culmen lengths of 97 adult male Sage Grouse in Gunnison and Jackson counties, Colorado, 1984–1986. Some points represent >one individual.

Results.—There were no differences ($P > 0.11$) in morphological features of adult males between early and late periods of courtship in 1984 and 1985. Because morphological characteristics did not vary between collection periods, data from adult males were pooled within years in each population.

Morphological features of adult males differed ($P < 0.0001$) between populations (Table 1). Body mass (minus ingesta) differed ($P = 0.003$) among years but in each year adult males in the Gunnison population weighed an average of 27% (688–736 g) less than adult males in North Park (Table 1). Body mass with ingesta was 26–28% (788–818 g) less for males in the Gunnison Basin. Carpal lengths also differed among years ($P < 0.001$) but were 10–12% shorter for adult males in Gunnison. There were no annual differences in tarsus and culmen lengths ($P = 0.22$ and 0.38, respectively). Tarsus and culmen lengths (pooled among years) were 7% and 23% shorter, respectively for males in the Gunnison Basin. A bivariate plot of culmen vs tarsus lengths indicated virtually complete separation between populations (Fig. 2).

Differences in body size were also apparent among females and yearling males (Table 2). Among these categories of age and sex, average live mass of Gunnison Sage Grouse was 26–30% lighter and carpal lengths were 8–11% shorter ($P < 0.001$) than for grouse in Jackson County. Tarsus and culmen lengths of yearling males were 8% and 20% shorter ($P < 0.002$) respectively, for grouse in the Gunnison Basin.

We examined data from other populations in Colorado to learn if morphological features of Sage Grouse in other areas more closely resembled grouse in North Park or the Gunnison Basin or if intermediate forms existed. Data on body mass were not available for most populations. However, measures of primary lengths of hunter-shot birds were available from seven areas of the state (Braun, unpubl. data). We compared average lengths of the outer and inner two primaries of adults of each sex with the Student-Newman-Keuls procedure. The primaries of both sexes were shorter ($P < 0.05$) in the Gunnison population relative to other areas. Primary lengths of females in other populations were similar to those of grouse in North Park. Primaries of males in Moffat County and the Piceance Basin were

TABLE 1

MORPHOLOGICAL MEASURES ($\bar{x} \pm$ SD) OF ADULT MALE SAGE GROUSE IN JACKSON AND GUNNISON COUNTIES, COLORADO, APRIL AND MAY, 1984–1986

Area	Year	N	Live mass (g)	Carcass mass (g)[a]	Tarsus (mm)	Culmen (mm)	Carpal (mm)
Jackson	1984	20	2885 ± 188	2561 ± 164	73.8 ± 2.6	41.0 ± 1.7	339 ± 8.0
	1985	20	2903 ± 156	2676 ± 150	74.5 ± 1.6	41.1 ± 1.5	340 ± 6.5
	1986	10	3005 ± 135	2718 ± 159	75.4 ± 1.6	41.0 ± 1.6	344 ± 5.8
Gunnison	1984	19	2070 ± 133	1873 ± 124	69.5 ± 1.1	32.9 ± 1.9	299 ± 5.8
	1985	18	2085 ± 133	1964 ± 101	68.9 ± 1.9	31.9 ± 1.2	304 ± 6.2
	1986	10	2217 ± 77	1982 ± 78.9	69.0 ± 2.3	32.8 ± 0.8	311 ± 2.6

[a] Live mass minus ingesta in the digestive tract.

TABLE 2

MORPHOLOGICAL MEASURES ($\bar{x} \pm$ SD) OF YEARLING MALE AND FEMALE, AND ADULT FEMALE SAGE GROUSE TRAPPED AND COLLECTED IN JACKSON AND GUNNISON COUNTIES, COLORADO 1983–1985

Age and sex	Area	Live mass (N)	Carpal (N)	Tarsus (N)	Culmen (N)
Yearling male	Jackson	2531 ± 182 (260)	328 ± 10 (151)	73.8 ± 3.8 (6)	38.9 ± 2.0 (6)
	Gunnison	1778 ± 133 (33)	293 ± 11 (35)	67.8 ± 2.0 (35)	31.1 ± 1.6 (35)
Yearling female	Jackson	1475 ± 118 (168)	277 ± 5 (29)	—	—
	Gunnison	1067 ± 77 (5)	251 ± 5 (5)	58.1 ± 1.2 (5)	27.8 ± 0.8 (5)
Adult female	Jackson	1626 ± 114 (143)	284 ± 6 (35)	—	—
	Gunnison	1210 ± 81 (13)	260 ± 9 (13)	58.6 ± 2.2 (13)	27.5 ± 1.2 (13)

TABLE 3
SPRING (FEB.–MAY) BODY MASS (KG) OF ADULT MALE SAGE GROUSE IN WESTERN NORTH AMERICA

Location	Source	Body mass (N)
Gunnison Co., Colorado	This study	2.1 (47)
Jackson Co., Colorado	This study	2.9 (50)
Jackson Co., Colorado	Beck and Braun (1978)	3.2 (465)
Moffat Co., Colorado	Braun (unpubl. data)	2.8 (39)
Eastern Idaho	Dalke et al. (1963)	2.5 (25)
Eastern Idaho	Autenrieth (1981)	2.6 (10)
Eastern Idaho	Autenrieth (1981)	2.5 (11)
Central Montana	Wallestad (1975)	2.9 (80)
Central Montana	Eng (1963)	2.9 (28)
Southwest Wyoming	Patterson (1952)	2.7 (31)

slightly shorter than those of birds in North Park but longer than those of males in the Gunnison Basin.

Discussion.—A seasonal difference in body mass was less apparent in our sample than in the larger sample of Beck and Braun (1978). However, in both populations, body mass changed annually. Winter severity affects body condition of Sage Grouse and may cause body mass to vary. The winter of 1983–1984 was especially severe in Colorado, and lipid reserves (Hupp and Braun 1989b) and body mass of adult males were lower than in other years. Carpal length also varied among years and suggests that growth and wear of Sage Grouse remiges may be influenced by environmental conditions (Pehrsson 1987).

We accounted for temporal differences in morphological measures of adult males and found the magnitude of variation within a population was much less than the difference between the two populations. We were unable to assess temporal differences in morphological measures for other categories of age and sex. However, differences between areas for adult females and yearlings of both sexes were comparable to those observed for adult males. Sage Grouse in all sex and age categories were significantly smaller in the Gunnison Basin than in North Park. Based on wing measurement data, Gunnison Sage Grouse are also smaller than grouse in other studied populations in Colorado. Comparisons based on primary lengths should be interpreted cautiously due to small sample sizes in some areas, and because primary length can vary among years (Table 1). However, these results suggest that Sage Grouse in other studied regions of Colorado most closely resemble birds in the North Park population and that intermediate forms do not occur.

We compared our data on body mass of adult males with that from studies of *C. u. urophasianus* in other regions (Table 3). Differences were apparent among regions, although we do not have estimates of variance for most populations. We could not account for temporal variation in estimates from other states; however, these data suggest that adult male Sage Grouse in the Gunnison Basin weighed approximately 400–800 g less than males in other populations of *C. u. urophasianus*.

In addition to the difference in body size that we observed between North Park and the Gunnison Basin, J. R. Young (unpubl. data) noted that acoustical and visual components of male displays on leks differed between these two populations. Acoustical elements of male displays in North Park were similar to those of populations in Montana and Wyoming

(Wiley 1973) and California (Gibson and Bradbury 1985), while displays of males in the Gunnison Basin differed from other studied populations.

The phenotypic differences of Sage Grouse in the Gunnison Basin are of interest, given the relatively close proximity (<100 km) of larger-bodied populations. Smaller body size of Sage Grouse in the Gunnison Basin may be due to random divergence of a genetically isolated population. We do not know if the Gunnison population is truly insular. While mountains surrounding the Gunnison Basin may create a barrier to gene flow, Sage Grouse have been observed in alpine areas (Hoffman and Cade 1982). Gene flow may occur between the Gunnison Basin and other unstudied populations that as a group are isolated from larger-bodied Sage Grouse.

We also do not know if there is an adaptive significance to smaller body size of Sage Grouse in the Gunnison Basin. It is unlikely that variation in body size is due to climatic differences between North Park and the Gunnison Basin as seasonal mean temperatures and precipitation are similar between areas (Natl. Oceanic and Atmos. Admin. 1983–1986). Differences in body size may have a nutritional basis as Sage Grouse in North Park and the Gunnison Basin feed on different subspecies of sagebrush that have dissimilar chemical composition (Remington and Braun 1985, Hupp 1987).

Insular populations of Sage Grouse may exist if individuals are unlikely to cross large areas that lack suitable sagebrush habitat. Morphologic divergence of isolated populations is possible. Populations in the southern portion of the Sage Grouse range have been studied less and appear to be more fragmented than populations in northern areas (Fig. 1). Morphological features and genetic divergence of populations of Sage Grouse in southern Utah and southwestern Colorado need to be examined and the extent of geographic variation determined for this species.

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Resting metabolic rate of Golden Eagles, Bald Eagles, and Barred Owls with a tracking transmitter or an equivalent load.—Solar-powered transmitters weighing 160–190 g have been used to track eagles and other larger birds by satellite (Strikwerda et al. 1986). This transmitter load, attached to the back of a bird, may increase the bird's resting metabolism by requiring greater tension in postural and leg muscles to support the additional weight, by increasing heat loss on the bird's dorsal surface in contact with the transmitter, or by increasing the stress level of the bird. Because the Bald Eagle (*Haliaeetus leucocephalus*) uses 90% of its daily energy when perched (i.e., during rest, Stalmaster and Gessaman 1984), even a small increase in the rate of resting metabolism would significantly increase daily energy expenditure and food energy requirements of the bird. We examined the effect of dorsally mounted loads on the resting metabolism of Bald Eagles, Golden Eagles (*Aquila chrysaetos*), and Barred Owls (*Strix varia*) in a series of three experiments over two years. The results from each experiment were used to improve the design of the next experiment; therefore, the methodology differs somewhat among the three experiments.

Methods.—The rate of oxygen consumption ($\dot{V}O_2$) of two Golden Eagles perched outdoors in a small aviary (2.6 × 2.6 × 4.0 m) was measured several nights in December, 1986, with and without a radio transmitter harnessed on their backs. The two eagles (GE1, body mass [M_b] = 4.3 kg; GE2, M_b = 3.9 kg) had been kept outdoors in a large fenced area at the Willow Park Zoo, Logan, Utah, for four years and were transferred to the smaller aviary at the zoo a few days before the metabolic measurements. The birds were fitted with a falconer's hood modified with an outlet tube (see Fig. 16.5 in Gessaman 1987) so $\dot{V}O_2$ could be monitored continuously by withdrawing air from the hood through tygon tubing. The tubing led into a heated building adjacent to the outdoor aviary and conducted the air in series through a H_2O absorber (Drierite), a diaphragm pump, a flowmeter (a rotameter), a CO_2 absorber (Ascarite), a H_2O absorber (Drierite), and an O_2 analyzer (Ametek S-3A) calibrated with atmospheric air. $\dot{V}O_2$ of a bird was computed from Eq. 4b of Withers (1977) and converted to rate of energy metabolism (H_m in W/kg) using the factor 19.8 kJ/L O_2. The eagle wore the hood for a few days before the $\dot{V}O_2$ measurements to habituate it to the hood.

During the $\dot{V}O_2$ measurements the eagle was perched either on the ground or on a log in the aviary. An eagle was harnessed with a transmitter several hours before the start of $\dot{V}O_2$ measurements in the evening. Some nights $\dot{V}O_2$ was monitored from 18:00 to 23:00 h with the transmitter on the bird. On other nights $\dot{V}O_2$ was monitored for two to three h with the transmitter on the bird and for another two to three h without the transmitter. In the second protocol the mean $\dot{V}O_2$ during the last hour of each of these two periods was stable and therefore was used in the subsequent analysis. Air temperature in the aviary was measured with a mercury-in-glass thermometer.

A harness that attached the transmitter to an eagle was worn during all $\dot{V}O_2$ measurements (i.e., with and without a transmitter attached). The harness was constructed of two loops of insulated 14-gauge solid copper wire, one loop fitting around the base of the neck, the other fitting around the body just posterior to the wings. The two loops were connected by similar wires running along the keel. The transmitter was secured to the bird with hooks and swivels attached to the dorsal part of the harness loops. The transmitter, developed by The Johns Hopkins Univ. Applied Physics Laboratory for tracking large birds using satellites (Strikwerda et al. 1986), measured 8.0 × 5.5 × 3.5 cm, weighed 192.5 g, and was solar-powered.

We measured heat flux density between the dorsal surface of the eagle and the overlying transmitter with a heat flux sensor (Thermonetics HA12-18-5-P). Heat flux density was measured with and without a 1 mm thick sheet of Goretex gasket material (manufactured from expanded or foamed P.T.F.E.) glued to the surface area of the transmitter (44 cm^2) in contact with the eagle. We measured heat flux density from the eagle in the absence of a transmitter by gently pressing the transducer against the dorsal surface of the bird.

A second experiment was designed: (1) to increase the number of mean $\dot{V}O_2$ measurements on each bird with and without an attached transmitter (4 to 6 for each condition), (2) to control air temperature, (3) to measure $\dot{V}O_2$ without using a hood, and (4) to obtain measurements of resting metabolism during the day, the bird's normal active period.

The resting metabolism of one immature (3.9 kg) and one adult (3.7 kg) Bald Eagle was measured with the birds unhooded inside a metabolic chamber in a temperature-controlled room at Utah State Univ. (USU). One side of the metabolic chamber (91.4 × 45.7 × 58.4 cm) was clear plastic, and the other sides were plywood. A perch covered with artificial turf was positioned 9 cm above the floor of the chamber; the bird's tail feathers just touched the floor. $\dot{V}O_2$ was recorded for 24 h at 0° and 15°C, with and without a transmitter attached to the bird's back. A transmitter was secured to the dorsal surface of an eagle using teflon ribbon (5 mm wide) in an X-attachment design (Snyder et al. 1989), i.e., an anterior neck loop and a loop posterior to the wings were joined over the keel of the bird. The longest axis of the transmitter was aligned with the anterior-posterior axis of the bird. The transmitter

extended 3.5 cm above the dorsal surface. The eagles were housed outdoors in a large fenced area at the Willow Park Zoo, Logan, Utah, and were transported to USU for 48 h for the $\dot{V}O_2$ measurements. Lighting in the chamber was controlled on a 12:12 photoperiod, lights turned on at 08:00 h (typical of the outdoor photoperiod at the time of the measurements).

In a third experiment, the equipment used in Exp. 2 also was used at the Raptor Center at the Univ. of Minnesota to measure $\dot{V}O_2$ of two captive Barred Owls. The owls were held at 20°, 0° and −20°C and were harnessed with three different loads: (1) an empty backpack weighing about 2% of the bird's body mass, (2) a backpack and lead weights inside weighing 5% of M_b, and (3) a backpack and lead weights inside weighing 10% of the M_b. A teflon ribbon harness, like that in Exp. 2, was used to hold a nylon sack on the bird's back. The sack was about 9.5 × 6.5 × 3.5 cm, weighed 15 g, and had a velcro flap closure on the top. Lead weights were added through the closure to adjust the load to 5% or 10% of each owl's M_b.

During a $\dot{V}O_2$ measurement, the unhooded owl perched inside a metabolic chamber (the same chamber used in Exp. 2) inside a temperature-controlled room. The rate of air flow through the open circuit system was 14 L/min. Twenty-four mean hourly $\dot{V}O_2$s were computed for each owl from a continuous 24-h recording of its oxygen consumption. These were control values, i.e., recorded without a backpack. $\dot{V}O_2$ of owls harnessed with a backpack was measured for 4–6 h at each of the three loads and was compared with the control rates measured earlier at the same hours. The lighting in the chamber was controlled on a 12:12 photoperiod; lights came on at 08:00 h. The average body mass of the two owls during the measurement periods was 812 and 745 g. They were probably both females.

Results.—In the first experiment mean rate of energy metabolism was not significantly different between the two Golden Eagles ($F = 2.36$; $P = 0.14$). The mean H_m of both eagles was about 17 to 18% greater when harnessed with a transmitter (Table 1). This increase was significant for GE2 ($F = 4.96$, $P = 0.049$, N = 11) but not for GE1 ($F = 1.167$, $P = 0.316$, N = 9). Mean hourly air temperature (T_a) in the outdoor aviary during the control and experimental measurements on GE1 averaged −12.5 and −12.7°C, respectively. T_a averaged −13.5 and −13.8°C during these same measurements on GE2.

In the second experiment mean H_m of two Bald Eagles without a transmitter at 0°C (2.01 W/kg) did not differ from that at 15°C (1.98 W/kg) ($F = 0.28$; $P = 0.598$). Mean H_m of both eagles without a transmitter during the day (2.04 W/kg; 08:00 to 20:00 h) was significantly higher than at night (1.94 W/kg; 20:00 to 08:00 h) ($F = 5.62$; $P = 0.018$). Mean H_m of eagles with a transmitter (2.04 W/kg) was 4.7% higher than without a transmitter (1.95 W/kg) ($F = 4.38$, $P = 0.037$) when all temperature data were combined. The mean H_m of transmitter-equipped birds at 0°C (2.18 W/kg) was 9.5% greater during the day the 12.7% more at night (2.04 W/kg) than controls (1.99 and 1.81 W/kg, respectively) ($F = 5.37$, $P = 0.0210$); however, H_m was not different ($P > 0.05$) between the control and transmitter-equipped birds at 15°C. Each eagle responded differently to transmitters at 15°C; the bird-temperature interaction was significant ($F = 11.23$).

H_ms of the two Barred Owls were analyzed with ANOVA by considering each owl, air temperature, and load as sources of variance. H_m values of the two owls were not significantly different. Mean H_m for both owls increased in the cold; 20°C = 2.64 (N = 77), 0°C = 3.45 (N = 77), and −20°C = 5.29 (N = 90) W/kg, respectively. The differences among temperatures were significant ($F = 110.7$). The H_m of owls wearing any of the three loads was not significantly different from the control rates of energy metabolism, i.e., without a load ($F = 1.0$).

Discussion.—Experiments 2 and 3 are the best tests of the effect of a large solar-powered transmitter and a variable-weighted backpack on the resting metabolic rate of an eagle and Barred Owl, respectively. The number of measurements of mean hourly $\dot{V}O_2$ was large in

TABLE 1

MEAN RATE OF ENERGY METABOLISM (±SD) (H_m IN W/KG) OF TWO GOLDEN EAGLES AND TWO BALD EAGLES WITH AND WITHOUT A 192.5 G SOLAR-POWERED TRANSMITTER HARNESSED ON THEIR BACK[h]

Experiment	Body mass (kg)	T_a (°C)	Energy metabolism			
					Calculated from allometric equations	
			Without a transmitter (control)	With a transmitter	Wasser (1986)	Aschoff and Pohl (1970)
Golden Eagle 1[d]	4.300	−12.6	4.33 ± 0.88	5.23 ± 1.22	1.70	2.34[f]
Golden Eagle 2[e]	3.900	−13.7	4.01 ± 0.66	4.74 ± 0.45	1.76	2.40[f]
Bald Eagles[a]	3.767	0 day[b]	1.99 ± 0.15	2.18 ± 0.21		
		night[c]	1.81 ± 0.22	2.04 ± 0.25		
		15 day[b]	2.04 ± 0.10	1.97 ± 0.09		3.08[g]
		night[c]	1.95 ± 0.13	1.98 ± 0.18	1.79	2.50[f]

[a] Data for 2 eagles are combined.
[b] Day = 08:00 to 20:00 h.
[c] Night = 20:00 to 08:00 hr.
[d] Golden Eagle 1 = GE1.
[e] Golden Eagle 2 = GE2.
[f] Inactive period.
[g] Active period.
[h] Measurements were made at different air temperatures (T_a in °C). The body mass of each bird was used with the allometric equations of Wasser (1986:61) for resting metabolism of falconiformes during the inactive period ($H_m = 34.62\ W^{-0.36}$, H_m in mW/g and W in g); and of Aschoff and Pohl (1970) for non-passerines during the inactive period ($H_m = 3.56\ W^{-0.266}$, H_m in mW/kg and W in kg); and during the active period ($H_m = 4.41\ W^{-0.271}$) to compute predicted rates of energy metabolism for comparison with the measured values.

Exp. 2 (N = 433) and in Exp. 3 (N = 244). The potential contribution of day to night changes in metabolism, on any observed differences between metabolism with or without a transmitter, was minimized or eliminated in both experiments. In Exp. 2, the rate of resting metabolism of two Bald Eagles harnessed with the solar-powered transmitter increased about 10% at 0°C but did not change significantly at 15°C. These results are supported by Exp. 1, where the metabolism of both eagles increased by 17% at −13°C. Therefore, at air temperatures of ≤0°C, the $\dot{V}O_2$ of a resting eagle under the conditions of this study will be higher when harnessed with the solar-powered transmitter.

In Exp. 3 the rate of energy metabolism of two Barred Owls at 20°, 0°, and −20°C was not significantly affected by wearing a backpack weighing 2%, 5%, or 10% of the bird's body mass. The tactile and visual stimulation of the backpack did not appear to stress the owls. The Barred Owls had been handled often as part of the educational program at the Raptor Center at the Univ. of Minnesota. The metabolism of the owls at 20°C (2.64 W/kg) was lower than that predicted by the Aschoff and Pohl (1970) allometric equation for non-passerines during the normal rest period (3.7 W/kg; $H_m = 22.42W^{-0.27}$, H_m in mW/g and W in g) but was similar to the value computed by the Wijnandts (1984:36) allometric equation for Strigiformes (2.61 W/kg) (BMR = $1.435W^{.759}$, BMR in kJ and W in g).

At air temperatures of 0°C and below, the metabolism of eagles wearing a metal box (i.e., the solar-powered transmitter) was higher than that of controls; in contrast, the metabolism of Barred Owls wearing a cloth backpack was the same as that of controls. These findings initially suggested to us that the increase in heat production of the eagles was a response to

an increased heat loss from the dorsal surface covered by the metal transmitter (the transmitter covered only about 2% of the eagles's surface area). However, heat losses through an uninsulated and an insulated transmitter, measured with a heat flux transducer were only about 7% and 2%, respectively, of the increase in heat production due to the transmitter.

The rate of energy metabolism of the two Golden Eagles in Exp. 1 was about two times greater than that of the Bald Eagles in Exp. 2. Two differences between Exps. 1 and 2 could account for part of the difference. The lower air temperatures in Exp. 1 should have elevated thermoregulatory metabolism, i.e., the heat required to maintain a relatively constant body temperature. Secondly, in Exp. 1, the birds wore a modified falconer's hood to collect respired gases. The hood may have imposed a higher rate of metabolism in two ways: (1) at times the tubing attached to the hood appeared to impose a twist on the eagles's head which could have increased tension and metabolism in neck muscles, and (2) the snugly fitting hood could have compressed some head feathers, reducing feather insulation and increasing heat loss from some surfaces of the head). In Exp. 2, the birds were perched in a roomy metabolism chamber, rather than wearing a hood.

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Sexual dimorphism and assortative mating in Black Terns.—Members of the family Laridae exhibit monomorphic plumage, and sex is difficult to determine by observation. In gulls, it is well-established that males generally are larger than females, and within mated pairs males are almost always larger than their mates (Shugart 1977, Ryder 1978, Fox et al. 1981, Hanners and Patton 1985). In terns, however, size dimorphism between the sexes has been documented only in Common Terns (*Sterna hirundo*) (Coulter 1986). Coulter (1986) also used these sexually dimorphic size traits to identify patterns of assortative mating in Common Terns. Patterns of assortative mating as it relates to body size have not been recorded for other Laridae. We report here on sexual dimorphic size traits and assortative mating of Black Terns (*Chlidonias niger*).

Methods.—In 1984, at Sycan Marsh, Lake Co., Oregon, individual Black Terns were captured in cylindrical nest traps (Dunn 1979). Thirty-seven terns, including 16 pairs, were trapped and sexed by laparotomy. We measured culmen length (CL) and total head length (THL-back of the head to the tip of the beak) with vernier calipers to the nearest 0.1 mm. We used paired *t*-tests to examine differences among pairs of known sex (Snedecor and Cochran 1980). An additional 88 pairs of terns were trapped and measured, but sex was not determined. For these 88 pairs, we assumed the tern with the larger total head length and culmen length within the pair to be the male and the smaller individual the female; this pattern of sexual dimorphic size traits within pairs of mated terns was consistent with the individuals of known sex in this study.

We used multivariate analysis of variance (MANOVA) with interaction to assess differences in the means of linear measurements between males and females and between groups of known sex individuals and of presumed sex individuals (SAS 1986).

Subsequently, we used the two morphological measurements of 37 terns of known sex to derive a discriminant function which predicted the sex of terns. We used Wilks stepwise discriminant function analysis (DFA) to identify the relative importance of the two variables, and we then used direct DFA which forced the inclusion of both variables to maximize the predictability of the discriminant functions (Klecka 1975). We used the 88 pairs that were sexed by their relative size within pairs as an independent sample and employed V1 validation procedures to test the accuracy of the discriminant functions (Frank et al. 1965, Fox et al. 1981). We examined patterns of assortative mating by assessing the Pearson correlation coefficients of the total head length and culmen length within each pair of mated terns.

Results.—For 16 mated pairs of Black Terns which were sexed by laparotomy, males had significantly larger total head length and culmen length than females (Table 1). Moreover, within each of the 16 pairs, males were always larger than their mates for both body traits.

Subsequently, we compared these two body traits for all Black Terns of known sex and the 88 pairs of Black Terns of presumed sex (Table 2). First, we tested for interaction between sex of terns (male/female) and method of sexing (known sex/presumed sex) and found no significant interaction between the two (MANOVA, $F = 1.098$, df = 2,208, $P > 0.336$). Second, we conducted a MANOVA without interaction and found there was a significant size difference between sexes (MANOVA, $F = 53.12$, df = 2,208, $P < 0.001$). Third, we conducted a second MANOVA without interaction between the two sample groups (known sex vs presumed sex) and found there was a statistically significant difference (but just barely) between the two groups (MANOVA, $F = 2.84$, df = 2,208, $P = 0.0493$). Using the two sexual dimorphic size traits, we generated two discriminant functions (Table 3). In both the Wilks and direct methods of DFA, total head length had the highest standardized discriminant coefficient (0.82 and 1.00, respectively) and was the most discriminating variable;

TABLE 1

MAGNITUDE OF THE DIFFERENCE BETWEEN MATED PAIRS OF BLACK TERNS OF KNOWN SEX (N = 16)

Characteristic	Mean difference[a]	SD	t[b]	P
Total head length (mm)	2.72	1.17	9.29	<0.0001
Culmen length (mm)	2.04	1.03	7.90	<0.0001

[a] Female from male.
[b] Paired t-test.

culmen length had a standardized discriminant coefficient of 0.22. The direct DFA resulted in the function with the highest accuracy (89%) of correctly classifying terns according to sex. This function for the 37 birds of known sex was:

$$41.80 = 0.63\text{THL} + 0.20\text{CL}$$

Terns with discriminant scores greater than 41.80 were classified as male, and terns with lesser scores as female. Using this function, 17 of 20 males (85%) and 16 of 17 (94%) females were correctly classified. When testing this function with the independent validation sample, however, only 78% (137/176) of the terns were correctly classified according to sex, 91% (80/88) of the females and 65% (57/88) of the males.

Patterns of assortative mating were evident for both total head length and culmen length (Figs. 1, 2). There were significant correlations for both linear measurements within mated pairs. The pattern was more pronounced for culmen length ($r = 0.34$, N = 104, $P < 0.001$) than total head length ($r = 0.21$, N = 104, $P = 0.032$).

Discussion.—Like gulls and Common Terns, sexual dimorphic size differences were also apparent in Black Terns and, similarly within mated pairs, male Black Terns were always larger than their female mate. The ranges of the two morphometric measurements employed here overlapped, however, and it was not possible to sex individual Black Terns on the basis of a single trait.

TABLE 2

MORPHOMETRIC MEASUREMENTS OF BLACK TERNS AT SYCAN MARSH, OREGON, 1984

	Males		Females	
	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD
Known sex				
Total head length[a]	20	59.60 ± 1.18	17	57.05 ± 1.44
Culmen length[b]	20	27.30 ± 1.14	17	25.37 ± 1.18
Presumed sex				
Total head length	88	58.83 ± 1.14	88	56.82 ± 1.25
Culmen length	88	26.59 ± 1.12	88	25.24 ± 1.11

[a] See methods for sex determination.
[b] All linear measurements in mm.

TABLE 3
DISCRIMINANT FUNCTION ANALYSIS FOR CLASSIFYING BLACK TERNS ACCORDING TO SEX, SYCAN MARSH, OREGON, 1984

Method	Variables available	Variables retained	Classification accuracy			
			Original sample		Validation sample	
			N	%	N	%
Wilks	THL[a], CL[b]	THL	37	87	176	79
Direct	THL, CL	THL, CL	37	89	176	78

[a] THL = total head length.
[b] CL = culmen length.

Interestingly, there was a significant differences in the size of the two body traits between the two sample groups (known sex vs presumed sex). Reasons for this are uncertain. The relatively small sample size of terns of known sex were all from a single nesting colony, while the larger sample of individuals of presumed sex came from nesting colonies throughout the study area. Intrapopulation differences in sizes were observed in Herring Gulls (*Larus argentatus*) (Threlfall and Jewer 1978), and possibly inter-colony size differences occur for terns nesting within the same localized breeding area. The discriminant functions for Black Terns yielded predictive functions which were lower (89% vs 94–99%) than similar functions derived for Herring Gulls (Shugart 1977, Fox et al., 1981), Ring-billed Gulls (*L. delawarensis*) (Ryder 1978) and Laughing Gulls (*L. atricilla*) (Hanners and Patton 1985). In those studies of gulls, total head length, and bill depth at the gonys generally were the best discriminating criteria.

Two factors may have contributed to lower predictive accuracies of the discriminant functions derived for Black Terns compared to gulls. One, Black Terns have poorly developed gonys on their bill, and though bill depth at the gonys is one of the most discriminating criteria in distinguishing the sex of gulls, it was not applicable to Black Terns. Second, we used only two measurements; additional variables might have improved the predictive accuracy.

Predictive functions for Black Terns were higher (89% vs 80%), however, than functions derived for Common Terns by Coulter (1986) who used bill depth, bill length, bill width, and body weight (but not total head length). Predictive discriminant functions for Common Terns might have been similar to those for Black Terns if total head length had also been included.

In Black Terns, the lack of agreement between the predictive accuracies of the original discriminant function and the V1 validation scores (89% vs 78%) may best be explained by the previously noted differences between the sample groups of known sex and presumed sex birds. The group of presumed sex individuals were slightly smaller ($P = 0.0493$) in morphometric traits than individuals from the group of known sex terns. When the linear measurements for individuals from the presumed sex group were inserted into the original discriminant function, the relatively smaller females in the presumed sex group were likely to have a discriminant score of less than 41.80 and be classified correctly. However, the comparatively smaller males from the presumed sex group were more likely than males of the known sex group to a have discriminant score of less than 41.80 and be classified incorrectly. Consequently, males in the validation group were incorrectly classified as to sex

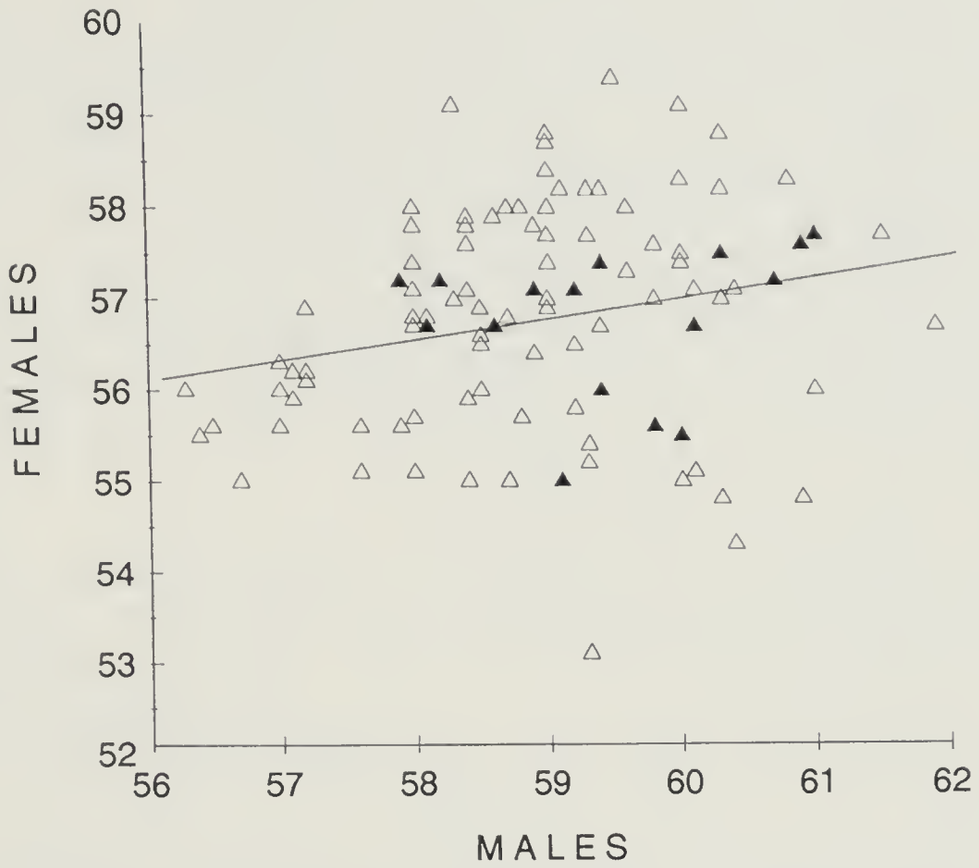

FIG. 1. Comparison of total head length (mm) between 104 pairs of mated Black Terns. Sixteen pairs were sexed by laparotomy (filled triangles) while the remaining 88 pairs (open triangles) were sexed by their relative size within mated pairs (males larger than females). Lines of best fit were determined by least squares regression ($r = 0.21$, N = 104, $P = 0.0032$).

35% of the time, while the error in misclassification for females was only 9%. Because of the differences in the two linear measurements between the two sample groups, the V1 validation was poor compared to the predictive values of the original function.

We assessed the limitations of having a small sample size from a single colony in the original discriminant functions by generating a second set of discriminant functions from the larger sized validation group (Table 4). The predictive accuracies of these functions (80–81%), however, were less than the original discriminant functions (87–89%). Thus, simply using a larger sized sample did not enhance the predictive powers of the discriminant function. Indeed, the lower predictive accuracies generated from the larger sample size indicate that a certain degree of variation may be characteristic of the population and that the degree of overlap in the size of the two sexes precludes 90–100% accuracy in distinguishing the sex of individuals throughout an entire breeding population.

In conclusion, Black Terns clearly were sexually dimorphic, and similar correlative patterns of sexual dimorphic size traits apparently exist in both gulls and terns. We suggest, however, that the sexually dimorphic size traits considered here in the Black Tern, a relatively small sized larid, are proportionately less pronounced compared to the larger species of gulls discussed previously. Accordingly, the measurements and discriminant function analysis techniques used to identify individuals by sex in larger gulls may lack the necessary precision to allow similar distinctions between the sexes in the small sized species of terns, particularly those which lack well-developed gonys (i.e., Black Terns and Common Terns). Investigation of sex dimorphic size traits in a small species of gull with poorly developed gonys (Bonaparte's

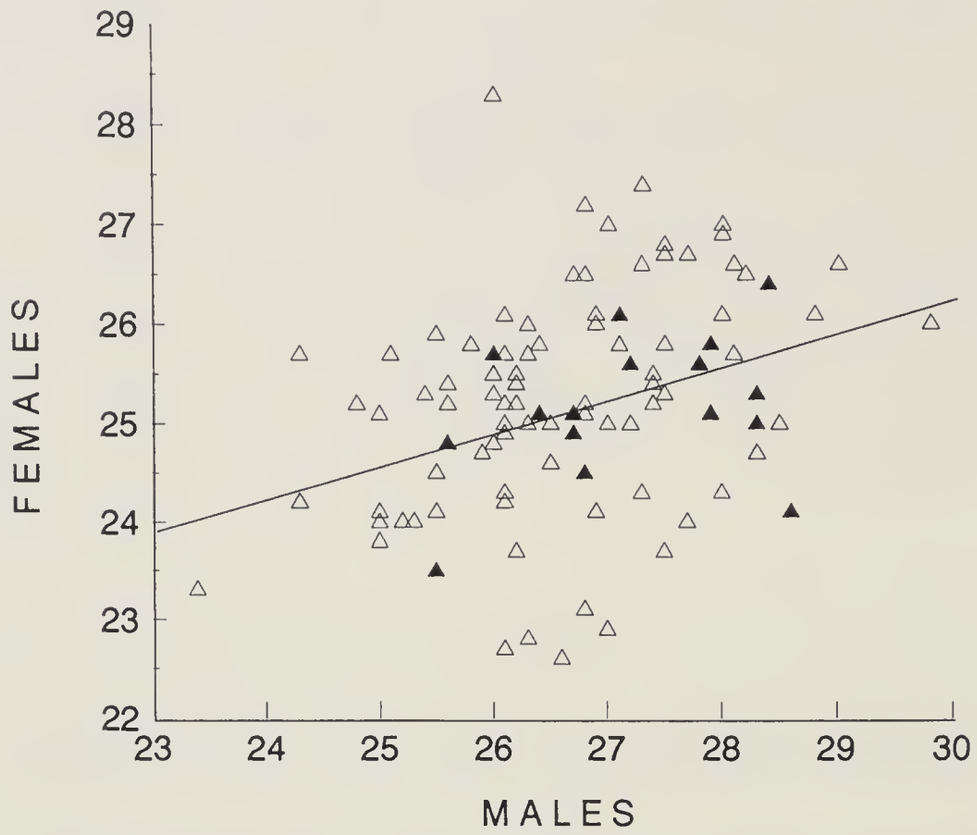

FIG. 2. Comparison of culmen length (mm) between 104 pairs of mated Black Terns. Sixteen pairs were sexed by laparotomy (filled triangles) while the remaining 88 pairs (open triangles) were sexed by their relative size within mated pairs (males larger than females). Lines of best fit were determined by least squares regression ($r = 0.34$, N = 104, $P < 0.001$).

Gull [*L. philadelphia*]) and a large species of tern (Caspian Tern [*Sterna caspia*]) would assist in further describing important sexual dimorphic size traits in larids.

Patterns of assortative mating for culmen length and total head length in Black Terns were similar to those observed in Common Terns (Coulter 1986). Coulter (1986) speculated that there is a positive correlation between age and size in Common Terns and suggested that Common Terns may, like other Laridae (Coulson and Thomas 1983, Nisbet et al. 1984), assortatively mate according to age. Thus, the pattern of assortative mating we found in

TABLE 4

DISCRIMINANT FUNCTION ANALYSIS OF A VALIDATION SAMPLE OF BLACK TERNS WHERE SEX WAS PRESUMED FROM THE RELATIVE SIZE OF MATES (MALES LARGEST)

Method	Variables available	Variables retained	Classification accuracy			
			N	Overall	Male	Female
Wilks	THL[a], CL[b]	THL	176	81%	84%	77%
Direct	THL, CL	THL, CL	176	80%	84%	75%

[a] THL = total head length.
[b] CL = culmen length.

Black Terns may be a function of a basic phenomena of assortative mating according to age in gulls and terns. Additional study of assortative mating by age and by size in Laridae is needed to clarify further these relationships.

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Diurnal activity patterns and foraging success of Yellow-Crowned Night-Herons in seasonally flooded wetlands.—The Yellow-crowned Night-Heron (*Nyctanassa violaceus*) has a New World distribution, occurring in a variety of wetland types including marshes, swamps, and lakes (AOU 1983). Although primarily associated with coastal regions and islands, certain populations exploit freshwater wetlands, including the middle Mississippi River and related tributaries (Hancock and Kushlan 1984). Detailed ecological studies of Yellow-crowned Night-Herons are lacking (Riegner 1982), and knowledge of habitat use and feeding strategies is largely restricted to coastal wetlands (Riegner 1982, Watts 1988, Custer and Osborn 1978). Information on Yellow-crowned Night-Heron use of inland freshwater wetlands consists mainly of food habit studies (Price 1946, Sutton 1967, Niethammer and Kaiser 1983). The objectives of the present study were to quantify diurnal activity and feeding patterns of Yellow-crowned Night-Herons and determine (1) the importance of seasonally flooded impoundments as foraging sites, and (2) if foraging differs among age classes and social statuses.

Study site and method.—Data on activity budgets and foraging by adult and immature Yellow-crowned Night-Herons were collected between June and August of 1980 and 1982 in seasonally flooded wetlands on Mingo National Wildlife Refuge (NWR), a 9312-ha hardwood wetland in southeast Missouri (Korte and Fredrickson 1977, Heitmeyer et al. 1989). About 635 ha of seasonally flooded wetlands are managed primarily for waterbirds. Herbaceous annuals comprise the primary vegetation in seasonally flooded wetlands with small, isolated areas of perennial vegetation occurring less frequently. The typical management strategy consists of annual spring or summer drawdowns (2–14 day duration) to promote growth of desirable plant communities adapted to germination and growth on mudflats (Fredrickson and Taylor 1982). The wetlands are flooded sequentially (<30 cm) from early fall through late winter, depending on the date of plant maturation and arrival of migrant waterbirds. Seasonally flooded wetlands, combined with open marsh habitat, constitute about 15% of all habitats in the Mingo Swamp (Heitmeyer et al. 1989).

Activity budgets were determined by instantaneous sampling procedures (Altmann 1974). Data were collected from automobiles or portable blinds, using a 15–40× spotting scope. Because birds were not marked to permit identification of individuals, some birds may have been observed more than once. The possibility of repeat observations is reduced, however, because we conservatively estimated the Yellow-crowned Night-Heron population using seasonally flooded wetlands at 200. Solitary Yellow-crowned Night-Herons and individuals selected randomly from flocks (2–20 individuals) were observed. Activity of the focal individual was recorded at 10-sec intervals using a metronome (Wiens et al. 1970). Nine activity categories were recorded: resting (loafing and sleeping), standing, walking, crouching, maintenance (preening and scratching), food handling, flying, drinking, and aggression. Activity categories were then grouped into foraging (standing, walking, crouching, or handling food) or non-foraging (resting, maintenance, flying, drinking, or aggression). Detailed data on foraging effort (attempts/h), foraging efficiency (captures/total attempts), prey type, and crayfish length (±1 cm) relative to heron bill length (±1 cm) also were recorded when possible. In addition, focal birds were classified as solitary or associated with flocks, based on the presence (flock) or absence (solitary) of at least one other ciconiiform within a 25 m radius.

The proportion of time each bird spent engaged in an activity was determined for each observation period. The data exhibited a non-normal distribution, based on the Shapiro-Wilk (W) statistic, and an angular (2*ARCSIN[SQUAREROOT X]) transformation was

performed prior to using parametric statistical analysis (Neter et al. 1985). The Shapiro-Wilk test indicated that foraging effort and foraging efficiency, also expressed in proportions, were approximately normally distributed, and no transformations were required.

The effects of age and flock on mean percent activity were assessed using 1-way ANOVA with two levels of classification. The effects of age, flock, and prey type on foraging activity were assessed using the same procedure. The folded form of the F statistic (F′) was used to test for equality of variance. When variances were unequal, the Cochran and Cox approximation was used to test for differences (SAS 1987). All results, unless otherwise stated, are expressed as weighted means.

Results.—Adult (N = 34 observation periods) and immature (N = 14 observation periods) Yellow-crowned Night-Herons were observed for 26 h 11 min and 12 h 2 min, respectively. Mean length of observation period/bird was 46.2 ± 4.7 min ([SE], range = 6 to 102) for adults and 51.7 ± 6.6 min (range = 24 to 91) for immatures. Five adults and six immatures were observed by themselves, whereas 26 adults and eight immatures were observed <25 m from other Yellow-crowned Night-Herons.

Activity budgets of adults and immatures were not different (Table 1). Time spent foraging averaged 87.1 ± 0.03% for adults (N = 34) and 81.8 ± 0.07% for immatures (N = 14) when solitary and flocked data were combined ($t = 0.68$, $P = 0.50$). When data were separated, based on flocked and solitary birds, activity budgets between age classes remained similar. Adults (N = 5) spent 95.2 ± 0.04% of time foraging compared to 68.5 ± 0.15% for immatures (N = 6) when alone ($t = 1.90$, $P = 0.10$). In the presence of other wading birds, adults (N = 26) and immatures (N = 8) averaged 84.8 ± 0.04% and 92.1 ± 0.03% of time foraging ($t = 1.29$, $P = 0.21$), respectively.

Food handling was the only activity that differed between age classes, when flocked and solitary birds were compared. Immatures (N = 8, $\bar{x} = 8.0 \pm 0.03\%$) spent more time engaged in food handling than adults (N = 26, $\bar{x} = 3.0 \pm 0.01\%$) when other Yellow-crowned Night-Herons were present ($t = 2.28$, $P = 0.03$). Although not significant ($t = 2.28$, $P = 0.10$), solitary adults (N = 5) engaged in food handling ($\bar{x} = 6.4 \pm 0.03\%$) more than solitary immatures (N = 6, $\bar{x} = 1.2 \pm 0.01\%$).

Adults (N = 34) spent more time engaged in foraging activities ($\bar{x} = 87.1 \pm 0.03\%$) than non-foraging activities ($\bar{x} = 12.9 \pm 0.03\%$), when all data were combined ($t = 15.23$, $P = 0.0001$). More time also was spent foraging ($\bar{x} = 95.2 \pm 0.04\%$) compared to non-foraging ($\bar{x} = 4.8 \pm 0.04\%$) when adults were alone (N = 5; $t = 11.13$, $P = 0.0001$) and in the presence of other wading birds (foraging = 84.8 ± 0.04%, non-foraging = 15.2 ± 0.04%; N = 6; $t = 11.51$, $P = 0.0001$).

Immatures (N = 14) allocated more time to foraging ($\bar{x} = 81.8 \pm 0.07\%$) than non-foraging activities ($\bar{x} = 18.2 \pm 0.07\%$) when all data were combined ($t = 5.72$, $P = 0.0001$). When separated into solitary and flocked birds, the amount of time spent in foraging ($\bar{x} = 68.2 \pm 0.15\%$) and non-foraging activities ($\bar{x} = 31.8 \pm 0.14\%$) was not different when immatures were alone (N = 6; $t = 1.50$, $P = 0.16$). However, immatures spent more time foraging ($\bar{x} = 92.1 \pm 0.03\%$) than non-foraging ($\bar{x} = 17.9 \pm 0.03\%$) when at least one other wading bird was present (N = 8; $t = 11.10$, $P = 0.0001$).

Detailed foraging data were collected on 36 Yellow-crowned Night-Herons (22 ad, 14 imm). Foraging effort did not differ between adults ($\bar{x} = 12.5 \pm 3.7$ attempts/h) and immatures ($\bar{x} = 18.4 \pm 6.1$ attempts/h) ($t = 0.82$, $P = 0.42$) when solitary and flocked data were combined. Foraging efficiency remained similar between age classes when data were separated into solitary ([ad: N = 4, $\bar{x} = 11.3 \pm 2.9$] [imm: N = 6, $\bar{x} = 10.1 \pm 6.4$], $t = 0.17$, $P = 0.87$) and flocked individuals ([ad: N = 15, $\bar{x} = 11.5 \pm 4.9$] [imm: N = 8, $\bar{x} = 24.7 \pm 9.3$], $t = 1.25$, $P = 0.24$).

Foraging efficiency (captures/attempts) of adults (N = 4, $\bar{x} = 75.0\%$) did not differ from

TABLE 1

DIURNAL ACTIVITY PATTERNS (PERCENTAGE OF TOTAL OBSERVATIONS) OF ADULT AND IMMATURE YELLOW-CROWNED NIGHT-HERONS ON MINGO NWR

Behavior[a]	Adult	Immature
Foraging		
Stand	63.9	54.9
Walk	13.7	15.4
Crouch	5.8	6.4
Handle food	3.7	5.1
Non-foraging		
Maintenance	3.1	5.8
Rest	8.3	12.3
Fly	0.9	0.6
Drink	0.3	0.2
Aggression	<0.1	0.0

[a] Behaviors were not different between age classes ($P > 0.10$).

that of immatures (N = 5, $\bar{x}$ = 71.3 ± 0.08%) when individuals foraged by themselves, but adults were more efficient (N = 14, $\bar{x}$ = 73.3 ± 0.07%) than immatures (N = 8, $\bar{x}$ = 51.1 ± 0.08%) when ≥1 conspecific was present (t = 1.93, P = 0.06). Adults also had a higher foraging efficiency (N = 14, $\bar{x}$ = 80.7 ± 0.05%) than immatures (N = 9, $\bar{x}$ = 56.5 ± 0.07%) when other species of herons were present (t = 2.96, P = 0.007). The overall foraging efficiency (solitary and flocked birds) of adults (N = 21, $\bar{x}$ = 77.1 ± 0.07%) was significantly (t = 1.97, P = 0.06) higher than that of immatures (N = 13, $\bar{x}$ = 58.9 ± 0.06%).

Prey types captured by Yellow-crowned Night-Herons included burrowing crayfish (*Procambarus* sp.), fish, tadpoles (*Rana* sp.), and one snake (Table 2). Relative crayfish length to heron bill length was significantly (t = 2.12, P = 0.04) greater for adults (N = 21, $\bar{x}$ = 1.15 ± 0.07) than for immatures (N = 12, $\bar{x}$ = 0.88 ± 0.12). When analyses were conducted on weighted means, tadpoles constituted a greater proportion of known prey taken by immatures than adults, whereas crayfish, fish, and snakes comprised similar proportions of known prey captured by adults and immatures.

Discussion.—Adult and immature Yellow-crowned Night-Herons spent similar amounts of time in foraging and non-foraging activities. Activity of immature Yellow-crowned Night-Herons was influenced by the presence of other herons. Solitary immatures spent an equivalent amount of time engaged in foraging and non-foraging activities, whereas foraging occurred more than non-foraging activities in the presence of other herons. An aggregation of herons may indicate a quality foraging site where prey densities or predictability of prey is great. Immatures in flocks may have foraged more than solitary immatures because they were in areas where prey densities were high. Also, foraging is, in part, a learned behavior (Kushlan 1981), and immatures in flocks may have been foraging at higher levels because they were learning from nearby conspecifics.

In contrast, adult Yellow-crowned Night-Herons performed foraging activities more than non-foraging activities regardless of flock size. Adult herons are more efficient at foraging and sometimes exhibit territoriality, particularly when prey are uniformly distributed (Kaiser 1982). Black-crowned Night-Herons (*N. nycticorax*) appear to use feeding sites repeatedly,

TABLE 2

WEIGHTED MEANS ($\bar{x} \pm$ SE) OF KNOWN PREY ITEMS (PERCENT) CAPTURED BY ADULT AND IMMATURE YELLOW-CROWNED NIGHT-HERONS ON MINGO NWR[a]

	Crayfish		Fish		Snake		Tadpole	
Age class	$\bar{x}$	(± SE)	$\bar{x}$	(± SE)	$\bar{x}$	(± SE)	$\bar{x}$	(± SE)
Adult[b]	76.7[A]	10.8	23.3[A]	10.7	0.0[A]	0.0	0.0[A]	0.0
Immature[c]	58.3[A]	14.9	11.1[A]	6.6	4.2[A]	4.1	26.4[B]	10.6

[a] Prey items sharing a letter between age classes did not differ ($P > 0.05$). Comparison by 1-way ANOVA with 2 levels of classification.
[b] N = 15.
[c] N = 12.

and individuals chase or evict conspecifics that land near them (Custer and Osborn 1978). This type of social behavior, combined with increased foraging efficiency, may permit exploitation of feeding sites by adult night-herons under any social condition.

Foraging effort (attempts/time), foraging efficiency (captures/attempts), and proportion of total time allocated to food handling were similar between solitary adults and immatures. Foraging effort also was similar when adults and immatures foraged in flocks, but adults foraged more efficiently, whereas immatures spent a greater proportion of total time engaged in food handling. These results indicate that immatures foraging in flocks are capturing fewer prey and spending more total time handling food than adults. This suggests that handling time per food item is likely greater for immatures foraging in a flock. The presence of other herons may displace immatures from favorable foraging areas or cause more inexperienced immatures to make foraging attempts prematurely before prey becomes inaccessible because of territorial boundaries.

Although Yellow-crowned Night-Herons are considered to be dietary specialists on crustaceans (Palmer 1962, Hancock and Kushlan 1984), the species and genera of prey vary among regions (Niethammer and Kaiser 1982, Watts 1988). Microhabitat conditions, including water depth, surface substrate, and vegetation, are important in determining the abundance, diversity, and distribution of prey (Willard 1977, Watts 1988). Habitat conditions favorable for tadpoles, as well as fish and crayfish, exist in seasonally flooded impoundments on Mingo NWR. During drawdown, these impoundments provide highly profitable prey complexes that are highly correlated to total wading bird use within portions of the Mississippi River basin (Reid 1989).

In our study, immatures had a more diverse diet than adults. Burrowing crayfish represented the primary prey captured by adults whereas tadpoles dominated the diet of immatures. Although crayfish contributed to the diet of both age classes, adults captured larger crayfish. Use of tadpoles by immatures may occur because this prey type is more readily available, smaller, and represents less dangerous prey for inexperienced birds, or is found within the same microhabitats as crayfish. In contrast, adults may pursue larger prey (i.e., crayfish and fish) because they forage more efficiently.

In conclusion, seasonally flooded emergent wetlands represent important foraging sites for Yellow-crowned Night-Herons. Foraging efficiency appears to differ between age classes, however, depending on social conditions. In the presence of other herons, immatures forage with lower efficiency. As a result, wetland managers interested in providing optimum foraging opportunities for herons of different ages should sequentially discharge water at slow rates

from impoundments comprising a wetland complex. Such a strategy will maximize the availability of shallowly flooded habitat over a longer time period, permitting greater dispersal of herons. Increasing dispersal may increase the foraging efficiency of immatures.

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Mate switching and mate choice in female Northern Mockingbirds: facultative monogamy.—Northern Mockingbirds (*Mimus polyglottos*) usually are considered monogamous (Laskey 1962, Ford 1983), and some pairs remain together for as long as eight years (Breitwisch, pers. comm.). However, several reports indicate that individual mockingbirds may breed opportunistically in a number of different mating combinations. The most commonly reported deviations from monogamy involve bigamous males that mated simultaneously with two females in adjacent territories, often following the disappearance of a neighboring male resident (Laskey 1941, Logan and Rulli 1981, Breitwisch et al. 1986, Derrickson 1989). Sequential polyandry, in which a female repeatedly paired alternately with two neighboring males within the breeding season, has also been observed (Fulk et al. 1987). I report here a number of instances indicating that female mockingbirds switch mates more often than initially expected for a "monogamous" species. Further, female choice is suggested by the variety of circumstances associated with mate switching.

In the breeding seasons of 1989 and 1990, I observed several instances of females switching mates in a residential population of mockingbirds in Guilford County, North Carolina. From 1 March–1 July, mating status and nesting success were determined by three to four visits per week to each of approximately 25 territories inhabited by mated birds. Eight to 10 territories inhabited by unmated males were visited biweekly. Each visit lasted from 5–10 min, and the status and behavior of each bird was noted. Instances of females switching mates fall into the following three groupings: (1) switches that followed the disappearance of the female's original mate, (2) switches in which a female resided in the territory of one male for a period with no indication of nest building or copulation, and then left his space to breed with a second male in a different territory, and (3) true re-matings involving banded females that nested with one male, left the territory in which he continued to reside, moved into the territory of and renested with a second banded male. The numbers below refer to these groupings.

(1) Female BkOBk switched mates both within and between seasons. From spring 1988–spring 1990 she successfully fledged young with at least three different banded males. Each switch followed the disappearance of the male residing in her territory, a pattern common when males disappear. However, this female appeared to be exercising female choice with each re-mating. In no case did a male move into her territory (common when females are widowed). Rather, each time she moved into the territory of her new mate. In early March 1989, she was seen in the territories of four different males. By late March, she remained with one male, with whom she successfully fledged young in 1989 and 1990.

(2) In autumn or early spring, four banded females left the territories of males with whom they had never been known to breed. Each moved into the territory of and nested with a different banded male. One showed the pattern seen before (Fulk et al. 1987), of moving freely across a territory boundary shared by two previously unmated males. In early spring 1990, she nested repeatedly with one of the males and remained with him throughout the remainder of the 1990 breeding season, despite two successive nest failures early in the season. The other male remained unpaired in his territory throughout the breeding season. Three other females were accepted into unmated males' territories in the fall, but moved to the territories of other banded males by the beginning of the next breeding season. Some females remained only a few weeks, but at least two stayed with their first males for three months before leaving. Because they probably never copulated with the first males they encountered, it would be inaccurate to claim that these females switched mates. However, their movements seem to indicate that female mockingbirds exhibit mate choice, leaving the territories of males that have accepted their presence and courted them for an extended period, to nest with other males.

(3) Across both years, true mate-switching, in which females copulated with one male and then renested with a second male while the original male remained in his territory, was seen in four of 33 (12%) of the females. In the first instance, female BROO moved between the territories of two males in 1989 and again in 1990. In 1988, she paired monogamously with her primary mate and spent the fall and winter in their territory. In March 1989, she moved between this territory and that of a newly arrived neighboring unpaired male. In sequence, she nested successfully with both. She first produced young with the second male, abandoned her young to his care at nestling day 11, and switched back to her primary male. Despite the failure of her 2nd, 3rd, and 4th nests, she remained with him through five successive nesting attempts and for the rest of the 1989 breeding season. The other male remained alone in his territory throughout the 1989 breeding season and for the fall and winter. She began the 1990 breeding season by again going back and forth across the males' territorial boundary. Once again, she mated first with her secondary male, but their nest failed, most likely due to cold weather. After the nest loss, her secondary male displaced the first male from his territory. She and her secondary male moved into the contested area, and she nested with him for the remainder of the season. Six of their seven nests were placed in her original territory, the space new to the male. Though he never returned to his original territory, the evicted male was seen in six different locations before June 1990, when he nested successfully with a widowed female four territories distant from his original space.

A second female, BRWW, experienced three unsuccessful nesting attempts with her original mate in their first season together. In each case, a new nest was completed but no eggs were laid. In April 1989, the female moved three territories away into the territory of a previously unmated male. She raised two successful broods with her second mate before he disappeared in May 1990. She remained in the territory for 5–6 weeks feeding two fledglings. During that period, a neighboring mated male moved into her territory and began courting her. Courtship chases, tandem flight, and male nesting displays all were seen before she left the territory, moved two territories away, and mated with a second already mated male. We saw no aggression among any of the females in these territories (e.g., Derrickson 1989).

In the third case, female RGR nested unsuccessfully with one male in 1987. She disappeared in summer 1987 and was rediscovered in spring 1990, having successfully reared young with a second male on the edge of the study area. Her original mate remained unmated from fall 1987 to spring 1990, when he successfully reared two broods with an unbanded female.

In the final instance of true mate-switching, an unbanded female nested successfully with

her primary mate and continued to feed young as she moved back and forth between their territory and that of a neighboring unmated male. Unlike female BROO, she consorted with her second mate while she and her first mate continued to feed nestlings. She copulated with the second male for her final brood of the season. Though he began nest construction just after her first brood of young fledged, she continued to feed her young and did not lay in the nest built by the second male until her fledglings were out of the nest for 14 days.

The differing fates of three females, each of whose mates disappeared in spring 1990, indicate variations in female mate choice. Among the "widows," female PPGR remained in her territory and mated with the male who moved into her territory after the disappearance of her original mate. This pattern is common in this and other populations (Breitwisch, Derrickson, pers. comm.). Female BRWW (see above) left her home territory after the disappearance of her mate, despite the courtship of an already mated neighboring male that expanded his territory into hers. She re-mated with a second already mated male several territories away. Female PBWP remained in her territory for three weeks during which an unmated neighboring male moved into her territory and actively courted her. Despite his extended singing and several nesting displays, the pair never nested, and the female eventually disappeared. Her return the following winter (after the male left) indicated that she indeed left and was not killed.

Females disappeared from the territories of three other mated males in 1990. In two cases, males remained with young which they successfully reared; the third followed a nest failure. While the fate of the females is unknown, it is possible that some moved into the territories of males outside the range of my observations. None of the males re-paired during the 1990 breeding season. This, and the presence of 8–10 territorial males who were unpaired throughout the season, indicate a male-biased sex ratio (seen in other populations as well).

In 1989 and 1990, a majority of the pairs in the population were monogamous, re-nesting repeatedly with the same individual. Seventy-eight percent (18 of 23) and 72% (18 of 25) of the pairings were monogamous throughout the breeding season in 1989 and 1990, respectively. These figures reflect only apparent monogamy (e.g., Gowaty 1985), and they include one male in 1989 and three in 1990 that were classed as monogamous, but that unsuccessfully courted other females after nesting with their primary female. The females of four pairs also classed as monogamous disappeared and were not seen again. For these reasons, the percentages may overestimate the frequency of monogamous pairings. In 1989, 22% (five of 23) females switched territories following active courtship with one male and nested with another male. Three of these each nested with two males within the breeding season. In 1990, 28% of the pairings deviated from seasonal monogamy either by male bigamy (three of 25 pairings) or by females switching territories after active courtship or mating with another male (three of 25 pairings).

Therefore, though many pairs were monogamous, some proportion of the females re-mated despite the original male's continued residence in the population. Others exhibited behavior suggesting that females visit the territories of several males, possibly comparing either characteristics of the territories held by the males or characteristics of the males themselves (Wittenberger 1983). Some females abandoned residency in what appeared to be a high quality home territory in which young had been reared successfully. For example, following the disappearance of her first mate, female BRWW reared her young in her home territory before leaving the territory and the male that occupied it. Although she may have been driven out by the mate of the encroaching male (Derrickson 1989), and since she had mated successfully in that territory, it is unlikely that territory quality alone was the basis of her action. Moreover, in August 1990, she returned alone to her original territory. Similarly, the female who repeatedly moved back and forth between the territories of two males

could have remained in the better of the two if territory quality were the only important dimension.

The occurrence of true mate switching indicates that some female mockingbirds continue to assess their mating choices even after they have paired monogamously for some time. Female BROO mated monogamously in 1988, before beginning a pattern of switching in 1989 and 1990. In addition, true mate switches did not necessarily follow nest failure. In 1989, female BROO abandoned old nestlings to move back into the territory of her primary mate. Further, she remained with him until the beginning of the next breeding season despite three nest failures and continued access to the adjacent male. On the other hand, female BRWW left following the construction of three nests in which no eggs were placed; after her departure both she and her former mate reproduced successfully with new partners.

Though the observations reported here may not apply to more northerly, migratory populations, these observations suggest that some female mockingbirds engage in active mate choice. The observations fit the pattern of successive comparison in female choice described by Wittenberger (1983). Successive comparison is consistent with the mockingbird's dispersed social structure, a male-biased sex ratio, the high level of male parental care typical of the species (Breitwisch 1989, Zaias and Breitwisch 1989), and the year-round territoriality seen in the southeastern United States (Logan 1987). Some females appear to reassess their mating decisions and, as a result, leave their original territory, opting to renest with a different male. It is possible that other females also repeatedly reassess, but opt to remain with their mates when the benefits of re-uniting with the same individual outweigh the costs of switching (e.g., Rowley 1983).

Mockingbirds may be preadapted for mate reassessment by the common occurrence of clutch overlap in this species (Logan et al. 1990). During clutch overlap, the female usually stops feeding fledglings, and the male assumes near complete feeding responsibility during the fledgling period (Zaias and Breitwisch 1989). Because the interval for renesting during clutch overlap depends upon brood size (Zaias and Breitwisch 1989), females with larger broods may be able to renest more quickly by switching to a male unencumbered by parental care. The costs of doing so would be minimized by a male-biased sex ratio. Such conditions would decrease the likelihood that her original male would re-mate, leaving her the option to switch back to her original mate. Consistent with this, Merritt (1985) and Derrickson (pers. comm.) have shown that when females are removed from a territory for a short period, no new females move into the spaces held by males. Finally, when parental load is lessened by decreased brood size, males may increase the likelihood of retaining the female by quickly beginning the nest for the next brood.

In this species, both males and females opportunistically deviate from monogamy. However, it appears that the opportunistic breeding of males is constrained by the demands of territory maintenance. We have no clear instances of mate switching in males, although bigamy is common. I suggest that mate switching is less common in males than in females because males are tied to the territory. Rather than risk losing space, the less costly option for males is to attract a second female or annex an adjacent territory containing a resident widow. In a population with a male-biased sex ratio, a female incurs little risk by leaving the territory of one male or, after being widowed, by opting to leave her territory when it is taken over by a new male.

The factors involved in mate choice in both males and females in this species are undoubtedly complex. However, these observations suggest that both female choice and mate reassessment occur in female mockingbirds. The coincidence in the species of polygamy in both sexes, mate choice and mate reassessment by females, and the maintenance of bonds for as long as eight years, suggest that the monogamy seen in mockingbirds is facultative

monogamy (sensu Ford 1983). That is, when no other opportunities present themselves, or when reassessment indicates that remaining with the same individual yields maximal benefit, monogamy prevails. However, the above observations suggest that this may entail considerable reassessment by females of the availability and value of other mating opportunities.

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Flock structure of wintering birds in an irrigated mixed-oak forest.—Wastewater (chlorinated effluent) irrigation in northern latitudes presumably can affect flock structure of wintering forest birds because of ice buildup on understory stems and lower branches of overstory trees and breakage of these foraging substrates (Sopper and Kardos 1973, Dressler and Wood 1976, Rollfinke and Yahner 1990). Although avian flock structure in winter has been studied in eastern deciduous forests (e.g., Morse 1970), nothing is known about how these aspects of wintering birds in eastern forests may have been altered by wastewater irrigation. In this study, we tested the hypothesis that flock structure (size and composition) of wintering birds did not differ between irrigated (with ice cover present versus absent) and nonirrigated forest stands.

Study area and methods.—Our study was conducted on a 200-ha section of State Game Lands (SGL) 176, Centre County, Pennsylvania, during the winters of 1986–1987 and 1987–1988. Forest stands were 50-to-65 years-old, and dominant overstory trees included white (*Quercus alba*), chestnut (*Q. prinus*), scarlet (*Q. coccinea*), north (*Q. rubra*), and black oaks (*Q. velutina*); red maple (*Acer rubrum*), bigtooth aspen (*Populus grandidentata*), and pine (*Pinus* spp). Major understory and shrub species included white sassafras (*Sassafras albidum*), black cherry (*Prunus serotina*), and red maple (see details in Rollfinke and Yahner 1990). The irrigation system consisted of about 3100 rotating sprinklers connected by a network of buried and surface lateral pipes. The system pumped up to 15 million L of wastewater daily (Matula 1983) and applied about 264 cm of wastewater to the soil annually, thereby tripling mean annual precipitation. Ambient temperatures in Centre County seldom fall below −18°C, and mean January temperature is −2.8°C (Matula 1983). Therefore, in the irrigated stand, appreciable ice cover (up to 15 cm thick and reaching 3–4 m in height above ground) often occurred on understory and ground-level vegetation when ambient temperatures were low (Rollfinke 1988).

We established four 250-m transects each in irrigated and adjacent nonirrigated forest stands. Transects were walked at a slow pace (≤1.5 km/h), and all birds heard or seen within a 50-m lateral distance of each transect were counted. Lateral distances from transects were at least 50 m from disturbances (i.e., unpaved roads) and habitat edges. Birds flying over the forest canopy were not counted. At the beginning of each count, temperature, percent cloud cover, precipitation, and wind velocity were recorded. Counts were not conducted during heavy precipitation or high winds (details of avian counts are given in Rollfinke and Yahner 1990).

Each transect was visited approximately twice per week from late December to early March in both winters. Birds were counted 24 times per winter along each transect at three times of day: eight times each in morning (07:00 to 11:00 h), midday (11:01 to 14:00), and late afternoon (14:01 to 17:30) (Rollfinke and Yahner 1990). When a flock of birds was encountered, numbers of individual birds and species composition were noted. A flock was defined as a group of two or more birds moving together (Morrison et al. 1987).

We compared the number of times each of eight common wintering species was encountered along irrigated and nonirrigated transects combined among three social-group types (solitary bird, single-species flock, and mixed-species flock) using *G*-tests for goodness-of-fit (Sokal and Rohlf 1981). Expected values were based on equal representation among social-group types. Pairwise chi-square tests-of-independence (Sokal and Rohlf 1981) were used to test for interspecific differences in frequencies of occurrence among the three social-group types. Mean (±SD) number of birds per mixed-species flock was determined for each common species and for all species combined. Mean (±SD) number of species and number

TABLE 1

NUMBERS OF OBSERVATIONS OF EIGHT BIRD SPECIES (PERCENT OCCURRENCE IN PARENTHESES) IN IRRIGATED AND NONIRRIGATED STANDS COMBINED, SGL 176, CENTRE CO., PENNSYLVANIA, IN EACH OF THREE SOCIAL-GROUP-TYPES: SOLITARY INDIVIDUALS, SINGLE-SPECIES FLOCKS, AND MIXED-SPECIES FLOCKS IN WINTERS 1986–1987 AND 1987–1988

	Social-group-type[1]		
	Solitary	Single-species	Mixed-species
Downy Woodpecker[a]	67 (42.7%)	12 (7.6%)	78 (49.7%)
Hairy Woodpecker[a]	30 (42.3%)	4 (5.6%)	37 (52.1%)
Black-capped Chickadee[b]	7 (8.0%)	14 (15.9%)	67 (76.1%)
Tufted Titmouse[c]	7 (14.3%)	1 (2.0%)	41 (83.7%)
White-breasted Nuthatch[bc]	12 (13.8%)	6 (6.9%)	69 (79.3%)
Brown Creeper[bc]	8 (11.3%)	6 (8.5%)	57 (80.3%)
Golden-crowned Kinglet[bc]	4 (4.9%)	8 (9.9%)	69 (85.2%)
White-throated Sparrow[d]	6 (13.6%)	22 (50.0%)	16 (36.4%)

[1] Observed versus expected number of observations were significantly different among social-group-types for each of eight species; G-test for goodness-of-fit, $G > 9.2$, $df = 2$, $P < 0.01$. Species with same letter in superscript were not significantly different among social groups, based on pairwise comparisons of species; chi-square test-of-independence; $\chi^2 < 7.0$, $df = 2$, $P > 0.05$.

of birds per flock were tested among flocks observed in the irrigated stand when ice cover was present (>50% of understory vegetation covered by ice, Rollfinke 1988), the irrigated stand when ice cover was absent (<50% ice cover), and the nonirrigated stand using single-classification analyses-of-variance (Sokal and Rohlf 1981). The percentages of mixed-species flocks containing each of the common species also were calculated.

Results and discussion.—Observed frequencies of the eight common bird species differed from expected among the three social-group types (Table 1). Five species were observed most often in mixed-species flocks and rarely as solitary individuals or members of single-species flocks. Downy Woodpeckers (*Picoides pubescens*) and Hairy Woodpeckers (*P. villosus*) were observed as single individuals nearly as often as they were found in mixed-species flocks. In contrast, White-throated Sparrows (*Zonotrichia albicollis*) were encountered more often in single-species flocks than in either of the other social-group types.

Four species (Downy Woodpecker, Black-capped Chickadee [*Parus atricapillus*], White-breasted Nuthatch [*Sitta carolinensis*], and Golden-crowned Kinglet [*Regulus satrapa*]) were present in over 50% of all flocks (Table 2). Black-capped Chickadees were the most abundant flock members, in terms of number of individuals per flock, and often led flocks. Mixed-species flocks of songbirds generally form around one or two nuclear species (usually parids), which possess a distinct system of alarm calls (Morse 1970, Gaddis 1980). Although Tufted Titmice (*Parus bicolor*) also were observed leading flocks in our study, they were found in a smaller percentage of all flocks than were chickadees, perhaps because of lower titmouse abundance (see Rollfinke and Yahner 1990).

White-throated Sparrows were observed in only 13% of all mixed-species flocks, yet they were found in larger numbers (up to 15 per flock) than other species. Downy and Hairy woodpeckers, White-breasted Nuthatches, and Brown Creepers (*Certhia americana*) always occurred in low numbers, e.g., never exceeding three individuals each per flock. Most woodpecker species maintain well-defined feeding territories throughout the year (Berner

TABLE 2

MEAN (±SD) NUMBER OF INDIVIDUALS OF EIGHT BIRD SPECIES IN EACH MIXED-SPECIES FLOCK, RANGE OF INDIVIDUAL BIRDS PER FLOCK, AND PERCENT (%) OF FLOCKS CONTAINING A GIVEN SPECIES, BASED ON 123 MIXED-SPECIES FLOCKS IN IRRIGATED AND NONIRRIGATED STANDS COMBINED, SGL 176, CENTRE CO., PENNSYLVANIA, IN WINTERS 1986–1987 AND 1987–1988

Species	Birds per mixed-species flock	Range per mixed-species flock	Percent of mixed-species flocks containing a given species
Downy Woodpecker	1.00 ± 0.89	0–3	63.4
Hairy Woodpecker	0.45 ± 0.77	0–3	30.1
Black-capped Chickadee	2.08 ± 2.40	0–9	54.5
Tufted Titmouse	0.71 ± 1.14	0–4	33.3
White-breasted Nuthatch	0.89 ± 0.90	0–3	56.1
Brown Creeper	0.67 ± 0.80	0–2	46.3
Golden-crowned Kinglet	1.39 ± 1.49	0–6	56.1
White-throated Sparrow	0.69 ± 2.29	0–15	13.0
No. species/flock	3.80 ± 1.86	2–10	—
No. birds/flock	8.20 ± 5.34	2–26	—

and Grubb 1985). If food supplies are adequate, a woodpecker often remains on its territory and joins a foraging flock only when the flock is within its territory. Thus, woodpeckers gain little or no advantage in finding food from participation in mixed-species flocks because they already are familiar with local food supplies (Berner and Grubb 1985). Rather, woodpeckers primarily receive anti-predation advantages, as evidenced by lower levels of vigilance when foraging with flocks of parids (Sullivan 1984). In contrast, tits, nuthatches, creepers, and kinglets do not maintain strict winter territories. Hence, by participating in vagrant flocks, these species benefit from improved chances of finding adequate food resources as well as from reduced time in predator surveillance (Morse 1970).

We observed 123 mixed-species flocks during the two winters. The occurrence of mixed-species flocks of wintering songbirds is a widespread phenomenon, especially in northern environments (Morse 1978, Morrison et al. 1987). Mean flock composition for mixed-species flocks in our study was 8.2 individual birds and 3.8 species (Table 2). Thus, mean flock size and species composition at SGL 176 compared closely with results from other studies: 10.1 birds, 2.5 species in Maine (Morse 1970); 6.2 birds, 3.6 species in Ohio (Berner and Grubb 1985); and 8.8 birds, 2.8 species in California (Morrison et al. 1987). Further, mean numbers of individual birds and species per mixed-species flock were not significantly different among the irrigated stand with ice cover present, the irrigated stand with ice cover absent, or the nonirrigated stand ($F = 0.97$; df = 2, 120; $P > 0.10$ and $F = 1.38$; df = 2, 120; $P > 0.10$, respectively).

Flock formation by songbirds may increase foraging efficiency and decrease predation risk for individual flock members (Sullivan 1984, Berner and Grubb 1985, Morrison et al. 1987). However, other factors, such as mate selection and thermal protection, can influence the decision to join a flock (Morrison et al. 1987). Increased avian participation in mixed-species flocks may be an adaptation to harsh environmental conditions, e.g., unfavorable weather

conditions or low food abundance (Morse 1970, Morrison et al. 1987). Conversely, when food resources are abundant, forest birds spend less time in flocks (Morse 1970, Berner and Grubb 1985). Hence, if winter ice cover in the irrigated stand of SGL 176 reduced food availability, birds would be expected to participate in flocks more often in ice-covered than in ice-free stands. However, because no differences were found in flock structure among the three treatments, we suspect that ice accumulation did not limit food availability appreciably for wintering birds on our study sites.

In conclusion, flock structure of wintering birds was not appreciably affected by wastewater irrigation. However, other studies have suggested that irrigation may increase avian density and diversity in both winter and the breeding season but may impact negatively those breeding species that forage and nest in leaf litter (Rollfinke and Yahner 1990).

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Summer diets of some introduced Hawaiian finches.—Approximately 25 species of finches (families Estrildidae, Fringillidae, Passeridae, Emberizidae) have been introduced to Oahu, Hawaii. Although at least 12 of these have failed to establish wild populations, 15 have been successful (Berger 1981, Pratt et al. 1987). Several reports have appeared regarding the diets of introduced finches in Hawaii, but we know of no comprehensive studies of diets of introduced finches in any particular habitat. For instance, Fleischer and Williams (1988) documented the use of discarded human food by House Sparrows (*Passer domesticus*), as did Bancroft (1982) for Red-crested Cardinals (*Paroaria coronata*). Ralph (1984) reported observations of four introduced finches: House Finches (*Carpodacus mexicanus*); Java Sparrows (*Padda oryzivora*); Northern Cardinals (*Cardinalis cardinalis*); and Nutmeg Mannikins (*Lonchura punctulata*) feeding at the flowers of a tiger's claw tree (*Erythrina variegata*) in downtown Honolulu. Paton (1981) observed gleaning by Yellow-fronted Canaries (*Serinus mozambicus*) on the island of Hawaii but unfortunately was not able to determine what food items the birds were taking. The goals of the present study were to study the diets of successfully introduced finches in urban parks on Oahu, Hawaii, to describe the diets of these birds, and to determine diet similarity among these species.

Methods and materials.—At least 13 species of introduced finches representing four families are known to occur in urban parks on Oahu (Ferris 1989). The families and their representative species are Emberizidae: Northern Cardinal, Red-crested Cardinal, Saffron Finch (*Sicalis flaveola*); Fringillidae: House Finch, Yellow-fronted Canary; Passeridae: House Sparrow; and Estrildidae: Red Avadavat (*Amandava amandava*), Common Waxbill (*Estrilda astrild*), Lavendar Waxbill (*E. caerulescens*), Nutmeg Mannikin, Chestnut Mannikin (*L. malacca*), Warbling Silverbill (*L. malabarica*) and Java Sparrow. Two other species of finches, the Orange-cheeked Waxbill (*Estrilda melpoda,* Estrildidae) and the Yellow-faced Grassquit (*Tiaris olivacea,* Emberizidae), have been introduced to Oahu but were not seen in the study by Ferris (1989).

We studied foraging of these species in urban parks along the southern coast of Oahu during the summers of 1983 and 1988. We made most of our observations in Kapiolani Park, Blaisdell Park, Sand Island State Park, and Campbell Industrial Park. In 1983, a few observations were also made at Keehi Lagoon Park and at the Woodlawn Cemetery in the Manoa Valley. In 1988, a few observations were made at Ala Moana Park. We chose these parks because they span the southern coast of Oahu, and previous field experience suggested that the majority of introduced species occurred in these parks.

We made observations through 10 × 50 power binoculars. Typically, birds of all species would stop foraging and freeze or flush if one approached too close. We attempted to record approximately equal numbers of separate foraging bouts for each species, but some species were seen too infrequently. During each bout, we recorded the number of bill strikes at each of six food-type/substrate categories. These categories were as follows: grass seeds on a plant; forb (=herbaceous dicots) seeds on a plant; sedge seeds on a plant; insects; garbage (=discarded human food); and fruit (=naturally occurring fallen fruit). The food-type categories we selected are crude, yet in our experience we felt they were adequate for establishing general patterns. In the field, we made tape recordings of each bout and later transcribed each bout.

We estimated proportional use of a particular resource in both years for each species by calculating the frequency of foraging bouts in which we observed at least one bill strike assignable to that resource. The use of proportions here reduces any potential bias due to interspecific differences in food size or feeding time (Ramsey and Marsh 1984).

TABLE 1

NUMBER OF FORAGING BOUTS PER SPECIES IN SEVEN URBAN PARKS FOR 1983 AND 1988

Species	Year	ALA[a]	BLA	CIP	KAP	SIP	KLP	WLC	TOTAL
Paroaria coronata	1983	—	0	2	16	1	0	0	19
	1988	5	3	0	5	7	—	—	20
Carpodacus mexicanus	1983	—	3	5	26	10	6	0	50
	1988	0	28	3	35	0	—	—	66
Passer domesticus	1983	—	1	2	21	2	3	0	29
	1988	1	11	0	7	10	—	—	29
Padda oryzivora	1983	—	0	0	21	0	0	8	29
	1988	0	8	0	55	0	—	—	63
Lonchura malacca	1983	—	48	5	0	0	0	0	53
	1988	0	51	2	0	0	—	—	53
L. punctulata	1983	—	0	0	21	33	1	0	55
	1988	0	0	2	55	3	—	—	60
Estrilda astrild	1983	—	0	35	0	0	0	0	35
	1988	0	0	21	0	0	0	0	21
Serinus mozambicus	1988	0	0	42	0	0	0	0	42
Amandava amandava	1988	0	0	4	0	4	—	—	8
Sicalis flaveola	1988	0	5	0	0	0	0	0	5

[a] ALA = Ala Moana Park; BLA = Blaisdell Park; CIP = Campbell Industrial Park; KAP = Kapiolani Park; KLP = Keehi Lagoon Park; SIP = Sand Island Park; WLC = Woodlawn Cemetery. A dash (—) indicates that the park was not visited during that year, whereas an '0' indicates that although the park was visited, no foraging observations for the species were made.

We estimated niche widths by calculating Levins' Measure (Levins 1968, Krebs 1989):

$$LM = 1/\sum (p_k^2)$$

Levins' Measure is the reciprocal of the sum of the squared proportions (p_k^2) for k food type categories. Lower values of Levins' Measure indicate relatively more specialized species, whereas higher values indicate more generalized species (Krebs 1989).

We determined similarity in dietary composition for each species-pair by calculating the coefficient of community (CC_{ij}), using the frequencies of use of the food-type/substrate categories. For these calculations, we used the formula provided by Ricklefs and Lau (1980):

$$CC_{ij} = \sum p \min (i \text{ or } j),$$

where CC_{ij} = the coefficient of community over all categories between species i and j and p min = the minimum shared proportion of species i and j for food type category k.

Results.—We recorded 637 separate foraging bouts for 10 species during the two field seasons (Tables 1 and 2). The species for which we were unable to obtain foraging observations were Northern Cardinal, Lavendar Waxbill and Warbling Silverbill. We found two fairly distinct foraging groups: grass-seed eaters, and forb-seed eaters. Eight of the 10 species can, with some caution, be categorized into one of these groups. The grass-seed eaters group includes the Java Sparrow, Chestnut Mannikin and Nutmeg Mannikin. It is likely that the Common Waxbill also belongs in this group. Although it fed chiefly on grass seeds in 1988, it mostly consumed sedge seeds in 1983. One possible reason for this shift is that Common

TABLE 2

TOTAL RECORDED FORAGING TIME, PROPORTIONAL USE OF SIX FOOD-TYPE CATEGORIES, AND SUMMER DIET BREADTH (LEVINS' MEASURE) FOR 10 SPECIES OF INTRODUCED FINCHES DURING 1983 AND 1988

Species	Year	TIME	FO[a]	IN	GA	GR	FR	SD	LM
Paroaria	1983	386.0	0.16	0	0.14	0.11	0	0	1.715
coronata	1988	332.4	0.55	0	0.35	0.10	0	0	2.298
Carpodacus	1983	1095.0	0.96	0	0	0.08	0	0	1.079
mexicanus	1988	717.7	0.94	0	0	0	0.06	0	1.127
Passer	1983	519.0	0.17	0.24	0.31	0.28	0	0	3.831
domesticus	1988	329.7	0.35	0.03	0.21	0.48	0	0	2.516
Padda	1983	593.0	0.21	0	0	0.83	0	0.03	1.363
oryzivora	1988	851.1	0.02	0	0	0.98	0	0	1.041
Lonchura	1983	1542.0	0	0	0	1.00	0	0	1.000
malacca	1988	659.6	0	0	0	1.00	0	0	1.000
L. punctulata	1983	1468.0	0.02	0	0	1.00	0	0	1.000
	1988	557.8	0	0	0	1.00	0	0	1.000
Estrilda	1983	531.0	0.03	0	0	0.40	0	0.69	1.560
astrild	1988	164.2	0.05	0	0	0.95	0	0	1.105
Serinus mozambicus	1988	478.5	0.71	0	0	0.31	0	0	1.656
Amandava amandava	1988	74.6	0	0	0	1.00	0	0	1.000
Sicalis flaveola	1988	76.6	0.80	0	0	0.20	0	0	1.471

[a] FO = forbs; IN = insects; GA = garbage; GR = grass; FR = fruit; SD = sedge; LM = Levins' Measure.

Waxbills may have only been recently introduced by 1983 (Falkenmayer 1988), and the total population size in that year may have been quite small. If so, our observations could have been biased. Most of our observations in 1983 came from a single flock of approximately 80 individuals at Campbell Industrial Park. Moreover, all of our observations were made in a period of just a few days. In 1988, our foraging observations for this species still were limited to Campbell Industrial Park but came from several different flocks scattered over several weeks.

It is possible that the Red Avadavat also belongs in the grass-seed eaters group. Unfortunately, our data (eight observations over 74.6 seconds) are too limited to make such an assignment. Nevertheless, the individuals that we did observe clearly fed on green grass seeds.

The forb-seed eaters group would include the House Finch, and the confamilial Yellow-fronted Canary. Some caution must be exercised in classifying the latter. All our observations for the Yellow-fronted Canary were from a very specific region of Kapiolani Park in 1988 where as many as 30 individuals of this species congregated in the early evenings near a stand of ironwood trees (*Casuarina equisetifolia*). If the total population of this species was small, our observations for this species could be biased as well. A third species that might belong in this group is the Saffron Finch, but we had only five observations (76.6 seconds), which would not be sufficient for us to unequivocally assign this species to any foraging group.

The Red-crested Cardinal and the House Sparrow do not appear to fit easily into one of the two foraging groups. In 1983 Red-crested Cardinals mostly consumed garbage. Indeed, 74% of the recorded foraging bouts for this species included at least one bill strike at some form of garbage. Individuals of this species also took grass seeds (11% of foraging bouts) and forb seeds (16% of foraging bouts). In 1988, however, we observed a shift in the use of two of these categories. The proportion of bouts that included the use of garbage dropped to 35%, whereas the use of forbs increased to 55% of recorded bouts. Interestingly, use of grass seeds was approximately equal in the two field seasons (1983—11%; 1988—10%).

Similarly, House Sparrows increased their use of forb seeds between 1983 (17% of bouts) and 1988 (34% of bouts). This species also increased its use of grass seeds between 1983 (28% of bouts) and 1988 (48% of bouts), while reducing its use of insects (1983—24%; 1988—3%) and garbage (1983—31%; 1988—21%). Since both species used a variety of food-types in both years, we feel it is safest to label these species as opportunists that are able to shift resource use to accommodate shifts in resource availability.

We limited our analysis of niche widths for the eight most common species, as indexed by Levins' Measure. Niche widths ranged from the most specialized with a low of 1.00 (Chestnut Mannikin, Nutmeg Mannikin, 1983, 1988) to a high of 3.831 (House Sparrow 1983, see Table 2).

Our results suggest that the majority of successful introduced finches tend to have relatively narrow diets. The House Finch, Chestnut Mannikin, Nutmeg Mannikin, and Java Sparrow all had small values for Levins' Measure in both years. The Red-crested Cardinal and House Sparrow had relatively higher values in both years, indicating somewhat broader diets. We must exercise caution when interpreting Levins' Measure with respect to the Common Waxbill and the Yellow-fronted Canary due to possible bias inherent in studying small populations. Nevertheless, Common Waxbills appeared to concentrate on grass seeds in 1988, when the total population was likely greater, whereas Yellow-fronted Canaries appeared, for the most part, to use forb seeds.

Coefficients for community for all species are listed in Table 3. Because overlap indices such as the coefficient of community are influenced by sample size (Ricklefs and Lau 1980), we also limited our overlap analysis to the eight most common species. In both years dietary similarity among species closely followed taxonomic relationships. Thus we found that the greatest similarity values were between congeneric species of the genus *Lonchura* (the Chestnut Mannikin, Nutmeg Mannikin) and the Java Sparrow. Moreover, if we ignore data for the Common Waxbill in 1983 for reasons previously discussed, high similarity values extend to all confamilial pairs. Thus, species in the family Estrildidae were most similar to each other.

In 1983, the House Finch was not particularly similar to any other species, although in 1988 it was most similar to the Yellow-fronted Canary. (There were no 1983 data for the canary.) However, if our 1988 data for the canary accurately reflect the diet of this species, the two members of the family Fringillidae also were most like one another.

Red-crested Cardinals and House Sparrows had their highest similarity with each other in both years, although in 1988 the Yellow-fronted Canary was equally similar to both these species.

Discussion.—Our results suggest two general and potentially important patterns. First, it appears that at least the summer diet widths of the majority of introduced finches are quite narrow. Second, similarity in diet appears to be associated with taxonomic similarity. These results both may hold only for urban parks and possibly only in summer.

In estimating diet composition of introduced species, one encounters several potential sources of bias in addition to the problems already mentioned as associated with small populations. One example involves the sampling of individuals in a single large flock, all feeding on an atypical food-type. In our data this might have contributed to the disparity

TABLE 3

COEFFICIENTS OF COMMUNITY FOR ALL POSSIBLE SPECIES PAIRS IN 1988 (FIRST LINE) AND 1983 (SECOND LINE). NUMBERS ACROSS THE TOP LINE CORRESPOND TO THE SPECIES LISTED IN THE FIRST COLUMN. AN "X" INDICATES INSUFFICIENT DATA FOR A COMPARISON

Species	1	2	3	4	5	6	7	8	9	10
1. *Paroaria coronata*	*	0.55	0.65	0.12	0.10	0.10	0.15	0.65	0.10	0.65
		0.24	0.58	0.27	0.11	0.13	0.14	X	X	X
2. *Carpodacus mexicanus*		*	0.34	0.05	0	0	0.05	0.71	0	0.80
			0.25	0.29	0.08	0.10	0.11	X	X	X
3. *Passer domesticus*			*	0.50	0.48	0.48	0.53	0.65	0.48	0.54
				0.45	0.28	0.30	0.31	X	X	X
4. *Padda oryzivora*				*	0.98	0.98	0.97	0.33	0.98	0.22
					0.83	0.85	0.46	X	X	X
5. *Lonchura malacca*					*	1.00	0.95	0.31	1.00	0.20
						1.00	0.40	X	X	X
6. *L. punctulata*						*	0.95	0.31	1.00	0.20
							0.42	X	X	X
7. *Estrilda astrild*							*	0.36	0.95	0.25
								X	X	X
8. *Serinus mozambicus*								*	0.31	0.91
									X	X
9. *Amandava amandava*									*	0.20
										X
10. *Sicalis flaveola*										*

in proportional food use between years seen in Common Waxbills and perhaps in Java Sparrows.

A separate problem could arise in species that are at once highly opportunistic and abundant. For such species diet composition would be largely dependent on resource availability. We believe that this is probably the case for the Red-crested Cardinal and House Sparrow.

Our results are all based on summer observations, and it is possible that some of these species change diet seasonally. Some species, particularly grass-seed eaters, are much less abundant in urban parks during winter, probably because of reduced availability of grass seeds (Ferris 1989). Unfortunately, we do not have quantitative data for all ten species to test the idea that seasonal shifts in resource availability and finch abundance are correlated.

We limited our study to urban parks and the question arises as to how applicable our results are to introduced finches throughout Oahu. The answer to this question rests on the importance of urban parks to introduced finches. If some of these species were more abundant in other habitats, one could argue that the diets of individuals in urban parks were atypical. A partial answer to the question of how important parks are to these species can be obtained by comparing the abundances of those species that were rare in parks to their abundances in other habitats. For those species that are more abundant in other habitats, the importance of parks could be negligible.

Of the 13 species in urban parks only five (Saffron Finch, Red Avadavat, Warbling Silverbill, Northern Cardinal, and Lavendar Waxbill) could be considered rare. Of these, the Warbling Silverbill recently invaded Oahu (Conant 1984). Of the remaining four species, two (Saffron Finch and Lavendar Waxbill) may occur only in urban or residential areas, and possibly only in urban parks. Only two species (Red Avadavat and Northern Cardinal) appear to be more abundant in other habitats. In our experience, Red Avadavats are more frequently encountered in agricultural fields, whereas Northern Cardinals are more frequently observed in both dry Kiawe (*Prosopis pallidus*) forests and wet forests. We also note that both species of introduced finches that we did not see in urban parks (i.e., the Orange-cheeked Waxbill and Yellow-faced Grassquit) occur in residential habitats (i.e., urban lawns) not included in our study.

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Intruders on Yellow-eyed Junco territories.—Yellow-eyed Juncos (*Junco phaeonotus*) are "apparently monogamous" and defend Type A territories within which all feeding, mating, and nesting activities occur (Hinde 1956). Both sexes chase same-sex adult conspecifics from the territory (Moore 1972, pers. obs.). Consequently, only male and female territory holders should be captured in local mist nets. However, we have captured 47 intruding adults since 1984. Here we examine the identity of these 47 birds, the conditions under which they were captured, and their status.

We have color banded Yellow-eyed Juncos in and around Rustler Park (31°55′N, 109°17′W) in southeastern Arizona since 1984. The study site (elevation 2560 m) is comprised of forest with little understory, areas of bracken fern (*Pteridium* sp.), short grass meadows, rocky outcroppings, and talus slopes. The predominant tree species are *Pinus ponderosa, P. strobiformis,* and *Pseudotsuga menziesii* (see Balda 1967 for a complete description of the study site).

We color banded nestlings 6–10 days after hatching. At this time we mist-netted territory holders, color banded unmarked adults, and replaced worn bands on banded adults. When capturing adult juncos at an active nest (172 occasions involving 144 nests) we erected 1–2 mist nets for 10–30 min within 1 m of the nest site. When capturing adults away from nest sites (90 occasions involving 58 territories, as part of on-going studies, Weathers and Sullivan 1989), we erected 5–8 mist nets on the territory for 1–4 h.

Since the end of the 1985 breeding season, we have routinely used playback tapes when capturing both male and female adult juncos. Tape recordings of local birds were played for 30 sec–1 min intervals near the mist nets. We alternated tapes of male song, nestling distress calls, female chipping, and fledgling begging until the desired bird was captured. If the desired bird was not captured within 3–5 min, we turned off the tape player, waited for approximately 10 min, then played the tapes again. If we still failed to capture the desired bird, we waited for 10–60 min and played the tapes a third time.

Captured adults were assigned to one of four categories: (1) territory owners, (2) intruding neighbors (birds from adjacent territories), (3) intruding local residents (territory holders

from the local population but not neighbors), or (4) intruding wandering birds (unbanded birds not seen again during the breeding season). Because the status of this last group was unknown, they could not be classified as floaters (Smith 1989) and instead were referred to as wandering birds. During the first year of this study, many of the local territory holders were not banded. We therefore excluded from the analysis of territorial status the three intruders captured in 1984.

The rate of intruder capture did not vary significantly among years ($\chi^2 = 4.54$, df = 5, $P > 0.05$; Table 1). Therefore, data from multiple years were combined in the following analyses.

The majority of intruders were males (41/47, 87.2%; Table 1). Wandering males represented 54.6% of the intruders captured. Local residents represented 11.4% of the intruders captured and were also exclusively male. Neighbors represented 35% of the intruders captured and consisted of three females and 12 males (Table 1). There was no significant association between a bird's status and whether it was captured at or away from a nest site (for both wandering and local resident males compared to neighbors, $\chi^2 = 0.05$ with continuity correction , df = 1, $P > 0.05$; for wandering males compared to neighbors, $\chi^2 = 0.02$ with continuity correction, df = 1, $P > 0.05$; Table 1).

Intruders were captured at nest sites in 21/122 (17.2%) netting attempts using playback calls while none was captured in 50 netting attempts without playback calls. Intruders were captured away from nest sites in 17/53 (32.1%) netting attempts using playback calls and in 9/37 (24.3%) netting attempts without playback calls. We were more likely to capture intruders when we used playback calls (38/175, 21.7%) than when playback calls were not used (9/87, 10.3%; $\chi^2 = 5.12$, df = 1, $P < 0.01$). We were also more likely to capture intruders away from nest sites (26/90, 28.9%) than at active nests 21/172, 12.2%; $\chi^2 = 11.17$, df = 1, $P < 0.01$).

Playback calls attract adult Yellow-eyed Juncos. This was especially noticeable when we were capturing adults at active nests, as we did not capture intruders at nest sites without playback calls. When nestlings are being fed, the nest site is the center of adult activity and may be the most heavily defended area in the territory. In addition, because we used fewer nets for shorter periods at nest sites, intruders would be less likely to encounter nets at a nest site than away from a nest site.

Although the majority of captured intruders were male, males juncos do not appear to be less wary or more attracted to playback calls than females. We used playback calls to capture resident juncos at 73 nests for blood sampling. On our first attempt, we captured both the male and female at 47 nests, only the female at 11 nests, and only the male at 15 nests ($\chi^2 = 0.75$, $P > 0.05$).

Yellow-eyed Juncos may "intrude" upon other juncos' territories for a variety of reasons related to their sex, territorial status, and mating status. In many passerines, conspecific intruders have been shown to be floaters (Smith 1978, 1989; Beletsky and Orians 1987), sexually mature birds prevented from breeding by the territorial behavior of other birds (Brown 1964). Unmated males, whether they possess a territory or not, may be searching for a territorial opening following the death of a resident male (indicated by the lack of a resident male, an unusual song on the territory, female chipping, or nestling distress calls). This population is slightly male biased because females experience higher predation rates during incubation and brooding than do their mates (Sullivan 1989). On three occasions, we observed a previously unmated male establish residence within 24 hours of the death of the original territory holder. One of these birds had been caught at two other territories prior to gaining a territory with a mate.

The mating status of wandering males was unknown, but based on the sedentary behavior of mated male juncos, they were probably unmated. Three of the local resident intruders

Table 1
Summary of Capture Records

Year	Mist net[a] location	Netting attempts	Intruders captured	Wanderers[c]	Local[b,d] residents	Neighbors[b,c]
1984	NS	27	0	—	—	—
	ANS	13	3 ♀	?	?	?
1985	NS	23	0	—	—	—
	ANS	25	7	3 ♂	1 ♂, 1 ♀	2 ♂**
1986	NS	34	3	3 ♂	—	—
	ANS	23	9	5 ♂	2 ♂, 1 ♀	1 ♂*
1987	NS	4	0	—	—	—
	ANS	7	2	2 ♂	—	—
1988	NS	46	9	5 ♂	4 ♂	—
	ANS	12	3	1 ♂	2 ♂	—
1989	NS	38	9	4 ♂	2 ♂,* 1 ♀	2 ♂
	ANS	10	2	1 ♂	1 ♂	—

[a] NS = nest site; ANS = away from nest site.
[b] Each * indicates one unmated male.
[c] Wanderers = Unbanded birds not seen again during the breeding season.
[d] Local residents = Territory holders from the local population but not from adjacent territories.
[e] Neighbors = Birds from adjacent territories.

held a territory but never had a mate during the breeding season. Two other local resident intruders were probably unmated. One of the neighboring male intruders was unmated throughout the breeding season. This bird was captured on two neighboring territories during the breeding season.

Both mated and unmated males may enter another bird's territory to attempt extra-pair copulations (Gowaty 1985). At the present time, we have no data on the frequency of extra-pair copulations in this population.

Mated neighboring birds may also enter a territory to investigate unfamiliar male songs (Weeden and Falls 1979). Additionally, neighbors may investigate disturbances, either to prevent predation on their own young or to assist their neighbors. Banding data indicate that siblings tend to establish territories near each other and that over 40% of the birds with one or more siblings in the breeding population share a territory boundary with at least one sibling (Sullivan, unpubl. data).

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Variable first prebasic primary molt in Rio Grande and Merriam's Wild Turkeys.— Gallinaceous birds typically retain the juvenal ninth (JIX) and tenth (JX) primary wing feathers during the first prebasic molt (Petrides 1945, terminology follows Humphrey and Parkes 1959). However, not all Wild Turkeys (*Meleagris gallopavo*) retain JIX and JX during this molt. Some retain only JX (reviewed by Lewis 1967), and in 21% of 125 Florida Wild Turkeys (*M. g. osceola*), all 10 juvenal primaries were molted (Williams and Austin 1970, 1988). Leopold (1943) suggested that Wild Turkeys were genetically predisposed to retain both JIX and JX, whereas domestic turkeys retained only JX. He further suggested that the frequency of this extended primary molt indicated the degree of cross-breeding between wild and domestic turkeys. Stable frequencies could be maintained if this molting characteristic had neutral selective value. Alternatively, Williams and Austin (1988) hypothesized that the first prebasic molt among wild birds varied in a genetically controlled manner along a north-south gradient related to climate. They predicted that more northerly populations would exhibit progressively higher frequencies of retention of both JIX and JX.

We examined patterns of first prebasic molt among winter-caught yearling (referred to as juveniles by some authors) Rio Grande (*M. g. intermedia*) and Merriam's (*M. g. merriami*) Wild Turkeys. Here we report our findings and discuss their relevance to the two stated hypotheses. Previous studies of first prebasic molt in Wild Turkeys primarily examined the Eastern (*M. g. silvestris*) and Florida subspecies.

Study area and methods.—Rio Grande Wild Turkeys were studied along the South Platte River in northeastern Colorado in 1986–1987 (Schmutz and Braun 1989). Merriam's Wild Turkeys were studied in southcentral Colorado west of Trinidad in 1986 and 1988–1989 (Hoffman 1990).

Turkeys were captured in January and February with drop-nets, cannon nets, and Clover single-gate deer traps. Captured birds were weighed to the nearest 500 g with spring scales. Numbers of juvenal primaries retained (identified by their greater wear and pointedness) were counted. Turkeys were classified as yearlings if JIX and/or JX were present, otherwise they were classified as adults. We assumed that molting of both JIX and JX by yearlings was rare or nonexistent, as it had never been reported outside of Florida. Primary length was measured from the rim of the follicle to the distal tip of the feather by placing a ruler behind the feather to be measured. The base of the ruler rested on the skin between the primaries and the feather was flattened against the ruler to remove its normal curvature. An index (GROW8) of the growth of the eighth basic primary (BPVIII) was computed as:

$$\text{GROW8} = (\text{LBPVII} - \text{LBPVIII})/\text{LBPVII} \times 100$$

where LBPVII and LBPVIII are the lengths of BPVII and BPVIII, respectively.

Wings were collected from males of both subspecies during the 1986–1988 spring hunting seasons. The four-week season began on the third Saturday in April. Age, number of juvenal primaries retained, and primary lengths were obtained when feather wear from courtship displays was minimal. Unless otherwise stated, all data and results pertain to yearlings.

Results.—Nineteen of 55 (35%) captured Rio Grande females and three of 17 (18%) captured Rio Grande males had molted JIX. Seven of 31 (23%) Rio Grande males shot during the spring hunting season had molted JIX. One of 27 (4%) female and none of 17 male Merriam's Wild Turkeys captured had molted JIX. Fifteen of 164 (9%) Merriam's males shot in spring had molted JIX. Overall, JIX was molted more frequently in yearling Rio Grande (28%) than in Merriam's Wild Turkeys (8%) (G-test, $P < 0.001$).

Growth of BPVIII was examined only in yearling females that retained JIX and JX, because those that molted JIX had already completed growth of BPVIII due to the sequential nature of primary replacement. We examined only females because of the small sample. Growth of BPVIII was apparently incomplete in Rio Grande birds ≤ 3.0 kg and for some Merriam's Wild Turkeys as judged by BPVIII's length relative to BPVII (Fig. 1, large index values meaning a large discrepancy in lengths of BPVII and BPVIII, and thus, a shorter than full-grown BPVIII). Growth of BPVIII was apparently complete in Rio Grande turkeys ≥ 3.2 kg as differences in proportional length between BPVII and BPVIII were approximately equal in all birds. We did not ascertain whether BPVIII was still growing. Rio Grande females >3.0 kg that had molted JIX were heavier ($N = 18$, $\bar{x} = 3.70$ kg, SD = 0.18 kg, one-way ANOVA, $P < 0.001$) than those that had not ($N = 29$, $\bar{x} = 3.47$ kg, SD = 0.21 kg, Fig. 2). Rio Grande adult females ($N = 24$, $\bar{x} = 4.06$ kg, SD = 0.29 kg) were heavier (one-way ANOVA, $P < 0.001$) than yearling females that molted JIX. Year differences were not significant in either ANOVA ($P > 0.49$).

Discussion.—Leopold's (1943) hypothesis for variable first prebasic molt required past or present hybridization between wild and domestic turkeys. We have no reason to believe that the two populations we studied were not pure, wild-strain turkeys. Plumage characteristics were consistent with their subspecific status. The few domestic birds that occurred on each study area were visibly different from the wild birds and were not seen to interact with them. Additionally, Leopold's hypothesis fails to explain molting of both JIX and JX by yearling Florida Wild Turkeys (Williams and Austin 1970).

The frequency of JIX molt among subspecies was in agreement with Williams and Austin's (1988) hypothesis. Both Rio Grande and Merriam's turkeys molted JIX less frequently than

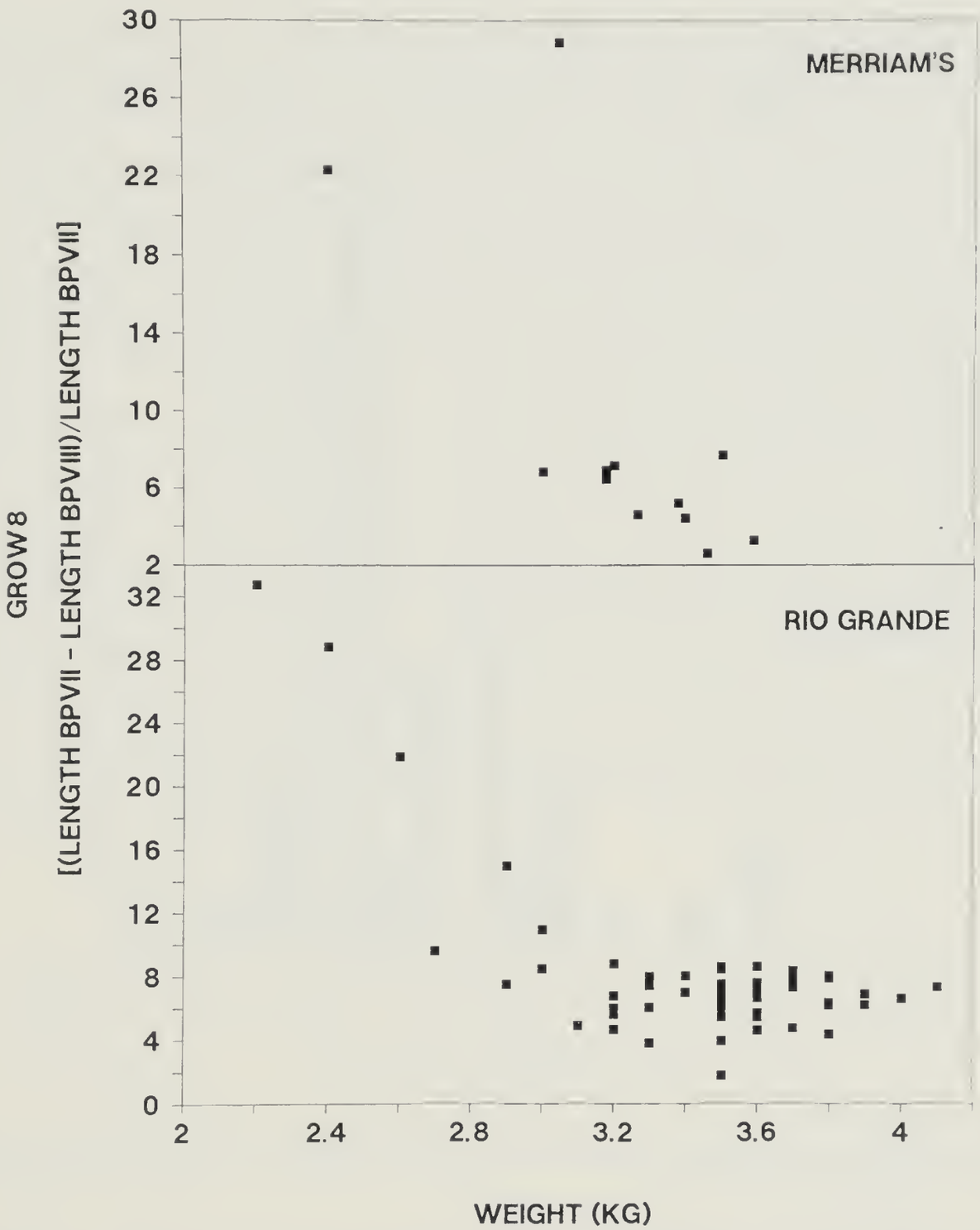

FIG. 1. Relative growth of the eighth basic primary (BPVIII) in female Merriam's and Rio Grande wild turkeys observed in mid-winter. Lower values of GROW8 are interpreted as more complete growth.

reported values for the more southerly Florida turkey (Williams and Austin 1988). The Rio Grande birds released in Colorado originated from Texas, Kansas, and Oklahoma, and occupy an area of milder climate than the native population of Merriam's turkeys within the state. Therefore, the higher frequency of JIX molt among Rio Grande as compared to Merriam's turkeys also supports the Williams and Austin (1988) hypothesis.

We then examined variation in extent of the first prebasic molt within a subspecific population. The extent of this molt was a function of body weight, which was likely correlated with hatch date. In this Rio Grande population, hatching occurred over an eight-week period

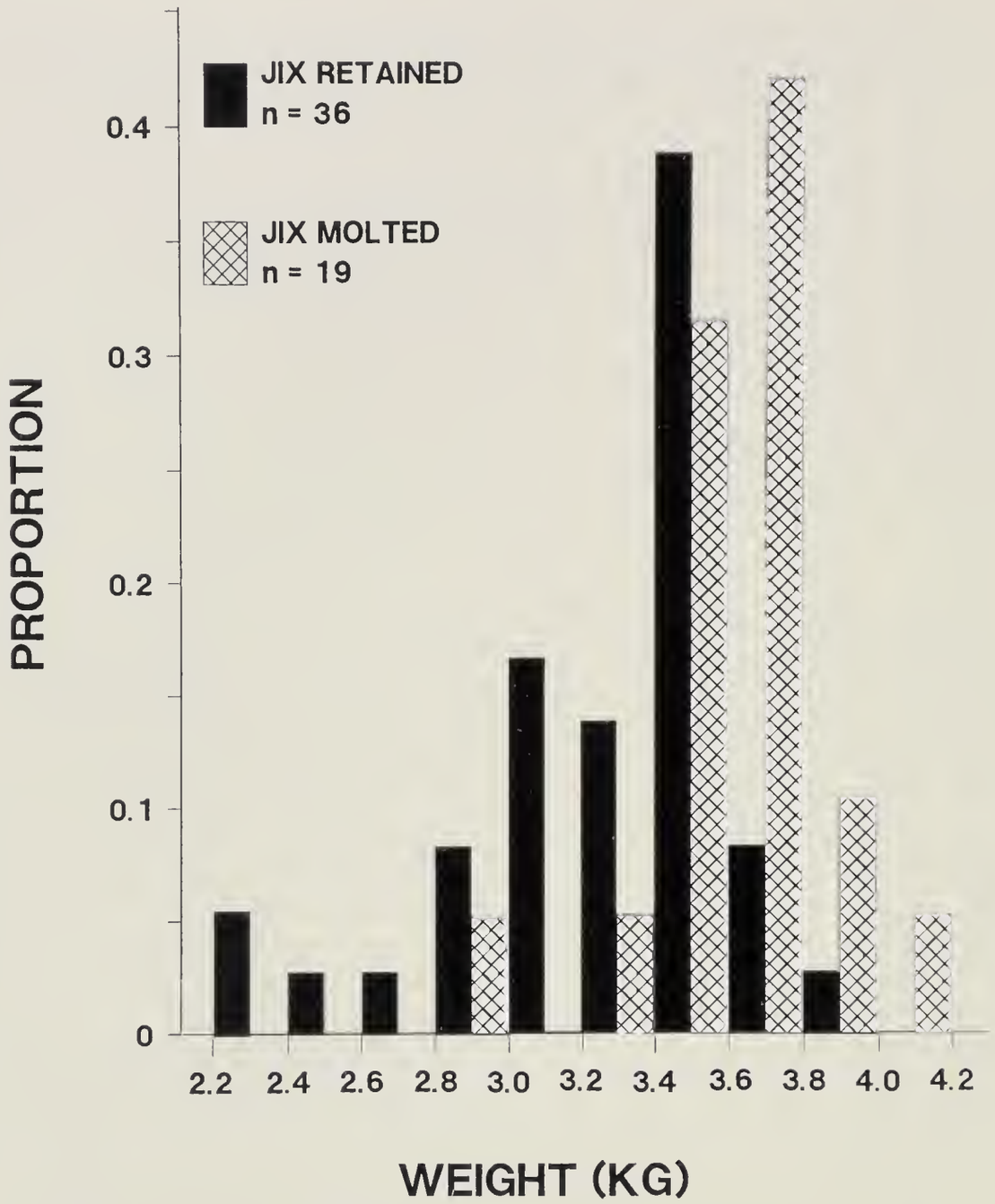

FIG. 2. Winter body weights (kg) of two molt classes of female Rio Grande Wild Turkeys.

(Schmutz and Braun 1989). This variation in hatching dates would result in a maximum age difference in days of about 25% among yearlings caught in early February. Yearlings that had molted JIX were heaviest and probably represented young from early nesting attempts the previous spring, assuming that body mass is closely associated with age. Yearlings that retained both JIX and JX, but apparently completed growth of BPVIII, were of moderate weight. Those that retained both JIX and JX and exhibited incomplete growth of BPVIII were lightest and probably represented young from late nesting attempts.

Merriam's turkeys also showed variation in extent of the first prebasic molt, but with a lower frequency of JIX molt. Yearlings in this population were younger than Rio Grande yearlings due to a month's difference in average hatch date (Schmutz and Braun 1989, Hoffman 1990), and had probably not progressed as far in the first prebasic molt.

Our assumption that body weight correlates with age among yearling Wild Turkeys is supported by Healy and Nenno's (1980) data on hand-reared Eastern Wild Turkeys, although their birds were younger. Mean female weights were strongly related to age for young 0–

189 days ($R^2 = 0.98$, $P < 0.001$) and 100–189 days ($R^2 = 0.94$, $P < 0.001$) of age. Given that heavier birds represent older birds, we have assumed that either onset or rate of the first prebasic molt is age-related. We believe that the onset of this molt is age-related in Wild Turkeys for several reasons: (1) the variable molt patterns seen in February among variable aged yearling turkeys suggested that convergence of the first prebasic molt, observed in Chaffinches (*Fringilla coelebs*) of different hatch dates (Dolnik and Gavrilov 1980), did not occur, (2) lengths of BPVII and BPVIII were strongly related to age in hand-reared Wild Turkeys (McGuire 1970, Healy and Nenno 1980), and (3) evidence for a relationship between age and molt onset has been observed in White-crowned Sparrows (*Zonotrichia leucophrys*, Morton et al. 1969, King and Mewaldt 1987). We know of no similar data within Galliformes.

Hens with BPIX and JX might be first-year adults that nested late, and, therefore, started molting later and either had not completed or prematurely terminated their prebasic molt by time of capture. Weight differences between hens classified as adults and those classified as yearlings with BPIX and JX argues against this hypothesis. Furthermore, this hypothesis does not account for variable molt among males.

The relative frequency of JIX molt among subspecies in this study supports the Williams and Austin (1988) hypothesis as an ultimate explanation of variation in the first prebasic molt of Wild Turkeys. However, our correlation of body weight, and probably hatch date (both partially influenced by enviromental factors), with the extent of first prebasic molt suggests that within a population the number of juvenal primaries molted may be subject to proximate environmental circumstances.

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Natal pterylosis of phoebes.—Detailed accounts of natal pterylosis currently are available for only a small percentage of the species of passerine birds of the world. The perception that natal down patterns have only limited value as taxonomic characters (Collins and Kemp 1976) and provide little information about concealing coloration or thermoregulatory ability has not engendered much support for further studies. As a result, the necessary specimens most often only are collected coincidental to other field studies (Marra 1990). As a result, the species coverage is spotty and is plagued by small sample sizes (Collins 1990). We present here data on three *Sayornis* flycatchers. This constitutes one of the few comparative analyses among all species of a single genus (see also Minsky and Collins 1983).

The genus *Sayornis* consists of three widespread and commonly occurring species of tyrant flycatchers: Eastern Phoebe (*Sayornis phoebe*), Black Phoebe (*S. nigricans*), and Say's Phoebe (*S. saya*). The breeding biology of all three species has been described by numerous authors (Bent 1942, Schroeder 1985 and references therein). All three species build shallow open-cup nests placed on a supporting structure, usually in a covered place, and in Eastern and Black phoebes, near water. Although many aspects of the breeding biology of phoebes is known in detail, the natal pterylosis has been described only for the Eastern Phoebe (Wetherbee 1957). As part of a continuing survey of natal pterylosis in passerine birds, we present here similar observations on both Black and Say's phoebes and review the pattern of natal pterylosis in the genus.

Wetherbee (1957:358–359; Table 4) reported information on the Eastern Phoebe based on 17 specimens collected in Maine, Massachusetts, Wisconsin and Michigan. Included were one late stage embryo, 10 newly hatched chicks (Stage A, Wetherbee 1957:356), five older chicks (Stage B) and one late-teleoptile stage chick with the sheaths of the pin feathers ruptured (Stage D).

Three Black Phoebe specimens were available for this study. A newly hatched chick (Stage A) and two early pin feather stage chicks (Stage C) were collected from nests on Rainbow Creek, San Diego County, California, on 17 May and 24 May 1983, respectively. An additional nearly fledged chick (late Stage D) was used for study of feather tract arrangement, but since down had probably been lost through abrasion, it was not included in the neossoptile counts for the species. Say's Phoebe was represented by two chicks (Stage B) collected from a single nest near China Lake, Inyo County, California, on 8 May 1974.

All specimens were examined under a binocular dissecting microscope and the number and distribution of natal downs (neossoptiles) in each species were recorded (Table 1). The terminology for neossoptile tracts and regions within tracts follows that of Wetherbee (1957).

TABLE 1

AVERAGE NUMBER (AND RANGE) OF NEOSSOPTILES PER TRACT OR REGION IN *SAYORNIS* PHOEBES

	Eastern Phoebe[a]	Black Phoebe	Say's Phoebe
Ocular	18 (13–22)	14 (13–14)	17 (15–18)
Infraocular	0 (0–1)	0 (—)	0 (—)
Coronal	14 (9–17)	11 (9–12)	13 (12–15)
Superciliary	0 (0–2)	0 (0–1)	0 (—)
Auricular	19 (16–20)	13 (12–14)	16 (13–18)
Postauricular	2 (0–5)	3 (1–4)	0 (—)
Occipital	10 (4–16)	6 (4–8)	10 (8–11)
Middorsal	10 (5–15)	5 (3–10)	9 (8–9)
Pelvic (medial)[b]	7 (5–9)	4 (1–6)	3 (3–3)
Pelvic lateral	0 (—)	0 (0–1)	1 (1–1)
Interscapular[b]	0 (—)	0 (0–1)	5 (3–6)
Scapular	12 (9–14)	7 (5–9)	13 (12–14)
Femoral	12 (10–13)	10 (8–13)	9 (6–11)
Ventral cervical	0 (0–5	0 (—)	0 (—)
Abdominal	14 (10–15)	10 (8–12)	14 (8–19)
Axillars	3 (0–5)	0 (—)	0 (—)
Crural	10 (6–12)	6 (4–7)	10 (8–12)
Rectrix	6 (6–6)	5 (4–6)	4 (1–6)
Upper rectrix coverts	4 (0–4)	2 (1–3)	4 (3–4
Primaries	0 (—)	8 (7–9)	9 (7–10)
Greater primary coverts	8 (5–9)	2 (0–6)	9 (8–9)
Secondaries	1 (0–3)	5 (1–9)	8 (8–8)
Greater secondary coverts	10 (10–10)	8 (8–8)	8 (8–9)
Middle secondary coverts	9 (8–10)	7 (5–8)	8 (6–9)
Carpal remex	1 (1–1)	1 (0–1)	1 (0–1)
Patagial coverts	0 (0–1)	0 (—)	1 (0–3)
Alula	2 (0–2)	2 (2–2)	2 (2–2)
Total average	337	254	340

[a] From Wetherbee 1957: Table 4.
[b] Unpaired region on midline (all others paired).

The Black Phoebes had 230–266 neossoptiles present in 18–21 tracts or regions while the Say's Phoebes had 319–349 neossoptiles present in 21–22 tracts or regions (Table 1). The total average number of neossoptiles (total of the average feather count for each individual tract and region) was 254 for the Black Phoebe and 340 for the Say's Phoebe (Table 1). The total average number reported for the Eastern Phoebe was 337 (Wetherbee 1957: Table 4). Say's Phoebe had, on average, neossoptiles present in 22 tracts or regions, while Black and Eastern phoebes had neossoptiles only in 20. All specimens of all three species of *Sayornis* had two or fewer neossoptiles present in the superciliary region; only the Eastern Phoebe had downs present in the infraorbital region of the capital tract. Both of these regions were first described as passerine neossoptile pterylae by Wetherbee (1957:350) in his study of the

Eastern Phoebe; the tracts appear to have adventitious downs present only occasionally in the genus *Sayornis* and have not been reported as containing downs in other recent studies (Minsky and Collins 1983, Collins and McDaniel 1989). The auricular region is strongly invested with neossoptiles in all three species of *Sayornis* and a few postauricular downs characterize two of the three species in the genus. These regions were similarly first described as passerine neossoptile pterylae in the Eastern Phoebe.

The pattern of neossoptiles we found in the regions of the spinal tract does not strictly agree with Wetherbee's (1957) description of the Eastern Phoebe. All specimens of all three species had 5–15 downs in paired rows in the middorsal region of this tract. Similarly, all specimens had 1–9 downs in an unpaired medial row in the pelvic region. However, Wetherbee (1957:350) noted that in the Eastern Phoebe the "two most posterior neossoptiles [of this region] were offset laterally." Similar offset downs in Say's and Black phoebes were not strictly posteriorly located, and they were therefore considered as belonging to a paired row of lateral pelvic region downs found on either side of the medial pelvic row. These lateral downs are only sparsely represented in *Sayornis* and are easily mistaken as part of the medial pelvic row. The lateral pelvic rows are well developed in other species such as the House Finch (*Carpodacus mexicanus*) (Collins and Bender 1977a) and Red-capped Cardinal (*Paroaria gularis*) (Collins and Bender 1977b); this is the first report of their being present in the Tyrannidae. Some *Sayornis* specimens also had unpaired medial neossoptiles at the anterior end of the middorsal region. There were 3–6 neossoptiles in this row in both specimens of Say's Phoebe and one down in one specimen of the Black Phoebe. This anterior medial row has perhaps been overlooked by other workers or considered as an asymmetric anterior extension of one of the lateral middorsal rows of neossoptiles. Its partial overlap with the anterior-most paired middorsal elements in one Say's Phoebe specimen demonstrates that it represents a newly recognized, but distinct, unpaired medial row of passerine neossoptiles which we propose to call the interscapular region of the spinal tract. The spinal tract is now considered to consist of interscapular, middorsal, pelvic (medial), and lateral pelvic regions. The paired dorsal cervical neossoptiles, recorded thus far only in the Red-capped Cardinal (Collins and Bender 1977b), could also be considered a region of the spinal tract, but it should be studied in additional species.

In *Sayornis,* as noted by Clark (1967) in nestling Red-winged Blackbirds (*Agelaius phoeniceus*) and in the genus *Amphispiza* (Minsky and Collins 1983), those individuals having the greatest number of downs also tend to have them present in additional pterylae. Despite this and some interspecific differences, natal pterylosis seems to be similar overall in the genus *Sayornis.* Examination of additional specimens of both Black and Say's phoebes would probably reinforce the sense of this similarity. Strong intrageneric similarity was also noted in *Amphispiza* (Minsky and Collins 1983).

Within the Tyrannidae, *Sayornis* nestlings have appreciably more neossoptiles present than an array of closed-nest building species, many of which have only sparse or no natal down at hatching (Collins and McDaniel 1989, Collins 1990). On the other hand, chicks of other open-cup nesting flycatcher species, particularly those nesting in more open situations (e.g., *Elaenia*) may have more than 500–600 neossoptiles (Collins, unpubl. data). The position of *Sayornis* along this continuum is appropriate for species that build open-cup nests in covered-over situations. This is an ecological rather than a taxonomic correlation as noted earlier (Collins and McDaniel 1989). The natal pterylosis of additional species deserves further attention before taxonomic implications are drawn or discarded for either the Tyrannidae or other passerine families.

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An incidence of second brood production by an Eastern Wild Turkey.—Renesting after loss of an initial nest has been well documented for Wild Turkeys (*Meleagris gallopavo*) (Williams et al. 1976, 1980). Based on a sample of 123 hens in Florida, Williams and Austin (1988) reported 57% renesting for hens that had their nests disrupted during the laying period, 28% for hens whose nests were disrupted during incubation, and no renesting after incubating more than 18 days. Turkeys are not known to renest following loss of a brood, and reports of Wild Turkeys hatching two broods in one season have not been published (Williams 1981). This phenomenon has only recently been documented for the Northern Bobwhite (*Colinus virginianus*), a species of the same family (Phasianidae) (Sermons and Speake 1987). We describe here the hatching of two broods in one season by a free-ranging Eastern Wild Turkey (*M. gallopavo silvestris*).

These data were collected during a study conducted in Thomas and Grady counties, Georgia. For a detailed description of the study area see Sisson et al. (1990). Reproductive efforts of 26 Wild Turkey hens were monitored from 1 March 1988 to 31 July 1990. Turkeys were captured in late winter with alpha-chloralose treated corn (Williams 1966), leg banded, outfitted with solar-powered radio transmitters with motion switches (Everett et al. 1978),

and released near the capture site. Hens were monitored daily to determine onset of incubation, at which time nests were flagged as described by Everett et al. (1980). Nests were located after hens departed to obtain data on nest success, clutch size, and nesting habitat variables. Hens successfully hatching broods were located three times daily to obtain data on brood habitat preference, and visual contact was made every two weeks to determine poult mortality.

Turkey #966 was one of 12 hens monitored during the 1990 reproductive season. Daily locations after winter flock break-up in late March revealed that #966 began continuous incubation of her first nest on 16 April. She was checked daily until she hatched her first brood on 12 May. Her nest containing 12 successfully hatched eggs was found on 14 May, at which time intensive telemetry monitoring was begun. On 18 May, we observed #966 crossing a fire-break with no poults. A second visual check on 21 May revealed she had indeed lost her entire brood. The fate of the brood was unknown. However, based on previous research (Speake 1980, Speake et al. 1985), the cause of the disappearance was assumed to be predation soon after hatching.

Since the primary focus of our study was on brood habitat and since Wild Turkey hens were not known to renest after losing a brood, #966 was not located again until 26 June during a random mortality check. Telemetry monitoring indicated no motion for this hen for two consecutive days at which time we decided to locate her visually under the presumption she was dead. However, due to the type of cover she was in and the close proximity of her location to the first nest site, we suspected a renest and carefully flagged her location on 27 June. Daily radio monitoring from close range indicated motion on 6 July, revealing she was indeed alive and incubating a nest. On 12 July she hatched her second brood as indicated by the nest that was found containing 12 eggs, 11 of which had hatched.

The nature of our data collection prevented obtaining absolute proof that the second nest #966 incubated was her own; however, we have no reason to believe it was not. To our knowledge the laying of an entire clutch by one Wild Turkey hen and incubation of that same clutch by another has not been documented, and probably does not occur. Williams and Austin (1988) reported that the potential for multiple nesting (defined as when more than one hen lays in the same nest) existed in Florida Turkeys (*M. gallopavo osceola*), but was probably not a common behavior and should be more prevalent when nest density was high. Our study was of a relatively low-density turkey population, and the nest in question was late in the season at a time when most nesting activity was over. Further evidence that this was her own clutch exists in the fact that the two nest sites were only 79.5 m apart, and the chronology of the two nesting events was right. If we assume that it takes 13 days to lay 12 eggs and 27 days for incubation (Williams 1981), then hen #966 would have had 16 days after the time of initial brood loss to begin laying another clutch. Sermons and Speake (1987) found an average of 13.5 days between brood disappearance and renesting for four Northern Bobwhites in Alabama. Based on the number of Wild Turkey hens monitored by telemetry since the mid-1960s, double broods are undoubtedly a rare occurrence.

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First nesting record for the Piping Plover in Oklahoma.—Piping Plovers (*Charadrius melodius*), endangered in the Great Lakes region and threatened throughout the rest of its range (U.S. Fish and Wildlife Service 1985), are known to nest in the northern Great Plains along the Loup, Missouri, Niobrara, and Platte rivers in Nebraska (U.S. Fish and Wildlife Serv. 1988). They often have been observed during both spring and fall migration at various sites in Kansas and Oklahoma but have never been known to nest in Kansas (Tordoff 1956, Johnston 1960, Thompson and Ely 1989).

During June and July 1986, a Piping Plover was seen at Optima Reservoir, located about 27 km east of Guymon, along the North Canadian (Beaver) River in Texas Co., Oklahoma (Fig. 1), but there was no indication of nesting.

On 17 June 1987, I found two adult Piping Plovers with four chicks along the west side of Optima Reservoir. The chicks were captured, measured, photographed (VIREO/VO6/7/001 thru VO6/7/004), and released. The adults were feigning injury. Neither was banded.

The Piping Plover chicks had been foraging along a sandy spit which projected into a shallow lagoon on the west side of the reservoir. A nest scrape of likely size, slightly larger and deeper than that made by Snowy Plovers (*C. alexandrinus*), but not as large as a Killdeer (*C. vociferous*) scrape, was discovered. The scrape was approximately 35 m from the water in loose sand and gravel. Snowy Plover chicks were seen farther north along the reservoir

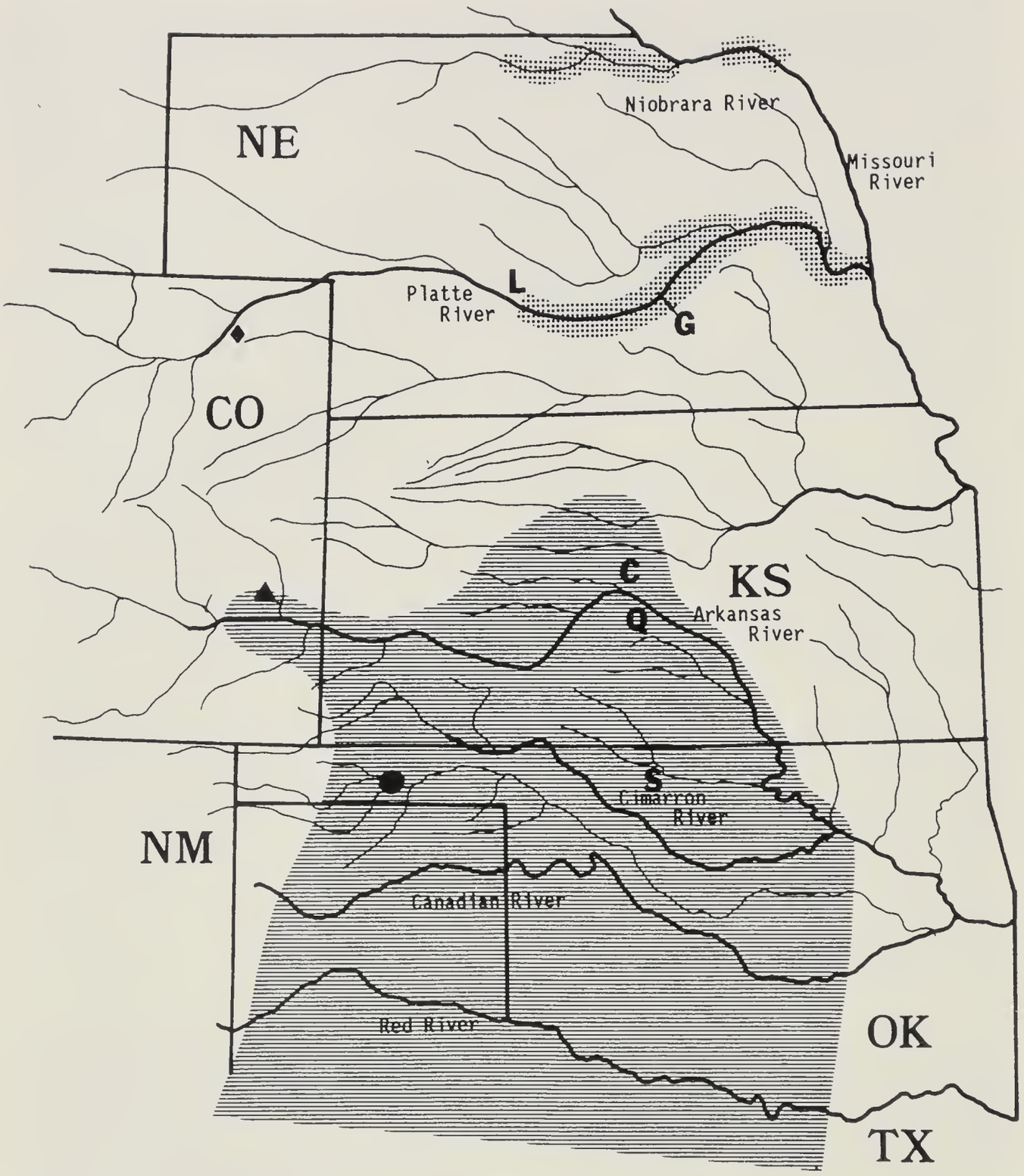

FIG. 1. Current breeding distribution of Piping Plovers in Nebraska (dots) and Snowy Plover (horizontal lines) in the southern Great Plains. Disjunct nesting records for Piping Plovers: Prewitt Reservoir (diamond), Nee Noshe Reservoir (triangle), Optima Reservoir (black circle). Other locations are Lexington (L), Grand Island (G), Cheyenne Bottoms WMA (C), Quivira NWR (Q), Salt Plains NWR (S). Piping Plover distribution from U.S. Fish and Wildlife (1988), Bailey and Niedrach (1965) and Kingery (1989); Snowy Plover distribution from A.O.U. (1983), Sutton (1967) and Boyd (1981).

shore, and an active Snowy Plover nest was found approximately 30 m north and closer to the water than the suspected Piping Plover scrape. On 26 June 1987, only one adult and two juveniles were located. I searched the west side of the reservoir on 7 July and did not find any adults or juveniles. I assumed that none of the juveniles fledged.

Comparing my measurements with those given by Cairns (1982) I estimated the juveniles to be approximately 8–10 days old. Based upon seven days for laying the clutch and 25–31 days for incubation (U.S. Fish and Wildlife Serv. 1988) I estimated the first egg was laid 2–9 May 1987.

During the summer of 1988, J. Shackford and others (pers. comm.) found three adult Piping Plovers and one active nest (25 June) at Optima Reservoir. This nest was inundated by heavy rains in early July and did not hatch. During the summer of 1988 and spring of 1989, water levels rose 4–5 feet higher than in 1987 and flooded all the favorable nesting habitat. No adults were seen during 1989 or 1990.

There is a single nest record for the Piping Plover along the South Platte River on 26 June 1949 at Prewitt Reservoir, Washington County, Colorado (Bailey and Niedrach 1965). More recently, there has been a sighting of a pair and four young on 28 June 1989 at Nee Noshe Reservoir, Kiowa County, Colorado (Kingery 1989). Other than these records, the closest current nesting record of Piping Plovers is along the Platte River between Lexington and Grand Island, Nebraska (U.S. Fish and Wildlife Service 1988) (Fig. 1). The nesting record at Optima Reservoir extends the known breeding range south of the Platte River by approximately 490 km.

This is the first record of Piping Plovers nesting sympatrically with Snowy Plovers (Fig. 1), but no interspecific interactions were observed. A possible reason that Piping Plovers have not nested in Kansas is that little nesting habitat is available. Major locations like Cheyenne Bottoms WMA and Quivira NWR, where Snowy Plovers nest in Kansas, are comprised of alkaline flats. Prindiville-Gaines and Ryan (1988) found that Piping Plovers favored sites with large amounts of sand and gravel. The nesting site at Optima Reservoir did consist of sand and gravel.

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Dirt-storing behavior by White-breasted Nuthatches.—In April and May 1989 and in March 1990, a pair of White-breasted Nuthatches (*Sitta carolinensis*) nested in two artificial cavities constructed from a seasoned cherry (*Prunus serotina*) trunk in Asheville, Buncombe County, North Carolina (for descriptions of the nest-sites, see Duyck and McNair 1991). During the nest building, egg laying, incubation, and nestling periods, the male nuthatch carried, stored and smeared pellets of dirt 1 cm below the bottom of the cavity entrance, both inside and outside of the cavity, and on the bottom lip. Bill-sweeping behavior as described by Kilham (1968, 1971) and Bancroft (1987) was observed. The male stored, and later retrieved, dirt on limbs and in the fork of a dogwood tree (*Cornus florida*), 3 m from the nest cavity. As late as five days before fledging in 1989, the male continued to store and smear dirt at the cavity entrance and store other portions of it and new pellets in the dogwood tree. This behavior was photographed by Duyck. Pellets were usually loose in composition although sometimes molded, 0.3–0.6 cm in diameter, and were collected from the forest floor within 10 m of the nests. When stored, the dirt was not covered by any object. Late in the nestling period in 1989, we noticed a few pellets of dirt on the cavity floor.

At 13:55 h on 17 March 1987, a pair of White-breasted Nuthatches was observed carrying nest material into an abandoned Red-cockaded Woodpecker (*Picoides borealis*) cavity near Ocoee Lake, Polk County, Tennessee. At 14:05 h, 75 m from the nest-site, one of the pair (sex unknown) landed on a 1.2 m high mound of fairly dry, reddish clay soil. The nuthatch pecked at the soil a few times, flew off with a solid 2-cm diameter piece, landed in a Virginia pine (*Pinus virginianus*), and stored the piece of soil in a bark crevice 1.2 m above ground. Upon inspection, we determined that no food was stored in the same bark crevice, and the soil pellet was not covered by bark chips or other material. When crushed, it did not contain any apparent food items.

The diameters of the cavity entrance at both the artificial cavity in 1989 and the old woodpecker cavity were larger, in at least one dimension, than the 3–4 cm diameter favored by White-breasted Nuthatches (Tyler 1948, Evans and Conner 1979, Raphael and White 1984). Thus, these nuthatch pairs may have been susceptible to cavity usurpation by larger intruders. Many species of nuthatches modify the entrance to their nest cavities throughout the breeding cycle (Rand 1972, Collias and Collias 1984:14–15). Some use dirt to plaster the cavity entrance to keep intruders out, and others construct a nest cavity almost entirely of mud (op. cit.). The diameter of the cavity entrance of the White-breasted Nuthatch pair at Asheville was not reduced by the male's dirt-storing and smearing behavior. Thus, the behavior in this case did not function to prevent intruders from entering the cavity.

Harris (in Tyler 1948) offers one clue as to the function of dirt-storing behavior in the White-breasted Nuthatch. He stated that a pair building a nest "collect little pellets of dried earth and lumps of mud which was scattered thinly over the bark (strips)" inside the nest cavity. We speculate that dirt may be used inside the nest cavity for sanitation purposes such as reducing ectoparasite loads. Storage of objects used for bill-sweeping, even at the cavity entrance, and storage of food items have been convincingly documented for this widespread North American species (Tyler 1948; Kilham 1968, 1974).

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Unusual behavior in a Solitary Vireo.—On 16 June 1990 (10:45 MST), we found a Solitary Vireo (*Vireo solitarius*) nestling on the ground at 1646 m elevation at the Southwestern Research Station (SWRS), Chiricahua Mountains, Cochise County, Arizona. The vireo was under a large sycamore tree (*Platanus wrightii*) along the north fork of Cave Creek. It had prematurely exited from a typical basket nest, suspended by its rim in the fork of tertiary branches, at the exceptional height of 12 m, approximately 6 m south from the trunk of the sycamore tree.

The parent(s) alternated feeding the nestling as well as juvenile(s) remaining in the nest. During the day, the grounded bird continued to hop around, begging by vocalizing and fluttering its wings. Vocalization periods of the fallen nestling generally lasted for 15–20 min and were followed by similar intervals of quiet. During one of the vocalization periods up to 30 chirps per min were noted. The parent(s) spent a large percentage of their daily time in feeding or foraging for the fledglings. At night, the fallen nestling took shelter under a cluster of small branches, remaining quiet until near sunrise. The vireos were all missing on the morning of 19 June, with no evidence of mortality.

Several of our observations appear to be unusual. First, we find few accounts of parents of this or other passerines continuing to feed a prematurely fledged, grounded bird along with siblings in the nest. Secondly, the height of the nest is of interest. Harrison (1979, A Field Guide to Western Birds' Nests, Houghton Mifflin Co., Boston, Massachusetts) found only one of 11 nests of this species above 3.1 m and no nests in riparian trees. Of the more than 200 Solitary Vireo nests reported on by Bent (1950, Life Histories of North American Wagtails, Shrikes, Vireos, and Their Allies, U.S. National Museum Bulletin 197) even notably high vireo nests were all under 9 m from the ground except for two 12 m nests (one for *V. s. plumbeus,* the subspecies breeding in the Chiricahuas, and one for *V. s. alticola,* breeding in the southeastern United States).

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ORNITHOLOGICAL LITERATURE

SPECIAL REVIEW

VOICES OF THE NEW WORLD NIGHTJARS AND THEIR ALLIES (CAPRIMULGIFORMES: STEATORNITHIDAE, NYCTIBIIDAE, AND CAPRIMULGIDAE). By J. W. Hardy, Ben B. Coffey, Jr., and George B. Reynard. ARA Records, P.O. Box 12347, Gainesville, Florida 32604-0347. 1989: 44-minute audio cassette, lengthy printed brochure with full documentation, color jacket photo of Gray Potoo (*Nyctibius griseus*) by R. A. Behrstock. $10.00.

VOICES OF THE NEW WORLD OWLS (STRIGIFORMES: TYTONIDAE, STRIGIDAE). By the same authors and publishers. 1990:65-minute audio cassette, full printed documentation, jacket color photo of Vermiculated Screech-Owl (*Otus vermiculatus*) by R. A. Behrstock. $10.00.—The printed brochures contain full scientific information on recording sources, recordists, dates, locations, and taxonomic evaluations. The combination of voices and documentation in systematic order is like a scientific monograph, but one in which a voice is worth a thousand words. Professional ornithologists will see that these two taxonomies overthrow the old system based on plumages. Bark and dry leaf patterns are too much alike to reveal relationships, while individual color differences exceed those between populations. The species on these cassettes are defined in the same way that the night birds recognize each other, by voice; and amateur ornithologists are given the means to identify the most difficult birds in the world.

The two cassettes evolved from a common ancestor, Hardy's (1980) "Voices of the New World Nightbirds," a long-play phonograph disc. That classic is remembered for Hardy's jacket cartoon worthy of a Picasso, and for inspiring all of us to fill the gaps. The three authors did the major field work, supplemented by bird tour leaders J. Arvin, R. Behrstock, S. Coats, T. H. Davis, D. Delaney, V. Emanuel, T. A. Parker III, J. and R. A. Rowlett, T. Schulenberg, and B. Whitney; regional or species specialists including W. Belton, M. Castelino, G. Clayton, D. Engleman, N. Johnson, C. König, J. C. and L. Magalhães, J. Marshall, J. P. O'Neill, R. S. Ridgely, M. Robbins, R. Straneck, J. Vielliard, J. Weske, E. O. Willis, and many other recordists and bioacoustic collections. Altogether 13 species of nightjars and 15 of owls, whose voices were unknown in 1980, were added to the original recording by Hardy.

Discovery came the hard way, after hilarious false starts, mistakes, and acrimonious debate by all of us. Like those erroneous 7-day incubation times that go back to Pliny, the bogus recording of the Northern Hawk Owl (*Surnia ulula*) goes back to the founding fathers of tape archives and has just been corrected by König. Mistaking the canopy tree-toad (*Anotheca*), for the voice of the Unspotted Saw-whet Owl (*Aegolius ridgwayi*) goes back to Irby Davis in the 1950s. Davis would mount the 42-inch parabola on the roof of his van before retiring to bed inside. When awakened by owls he would turn on the Nagra III tape-recorder, put on his headphones, and focus the parabola by turning a crank. He had to guess the identity of the singer outside in the dark. He guessed right most of the time, but his "Costa Rica mystery owl" was reincarnated in recent contributions to the night bird cassettes. Finally D. Delaney taped the real *Aegolius*, unmasking *Anotheca*.

In Yucatán, Davis switched songs between the Yucatán Poorwill (*Nyctiphrynus yucatanicus*) and the Yucatán Nightjar (*Caprimulgus badius*); it took the combined talents of J. Pierson, R. A. Rowlett, and B. Whitney to set things straight (Hardy and Stranеck, Condor 91:193–197, 1989). The mellow trill of Belton's male Long-tufted Screech-Owl (*Otus sanctaecatarinae*) from Rio Grande do Sul (Frontispiece) was summarily dropped from early versions of the owl cassette because J. Vielliard insisted it is the peracnema toad (*Bufo*

peracnemis). Sure enough, Hardy's sonagrams of the toad and owl are remarkably similar; nevertheless, Belton confirmed that he recorded an owl moving about in the trees, and the call is now restored to the cassette.

We were bamboozled by the angry calls (still on the cassette) representing *O. sanctaecatarinae, O. atricapillus,* and *O. hoyi.* Behrstock and Marshall thought they all were *O. sanctaecatarinae,* so they went to São Paulo in August 1989 to clear up the toads and to confirm *O. sanctaecatarinae* at Fazenda Barreiro Rico. Afterwards, they would discover the unknown song of true Nattererian *O. atricapillus* in Paraguay, as collected by Mercedes Foster at Cerro Corá National Park (Frontispiece). To the rescue! What they actually found were the same birds, true *Otus atricapillus,* at both places and their songs were the pure, musical trill of *O. guatemalae*! The strident voice from Barriero Rico that had deceived us was the apoplectic female *O. atricapillus* responding to territorial invasion. Such provoked songs are useless for taxonomic comparisons because they vary almost infinitely in complexity, overtones, and expansion of (instantaneous) pitch range as the angry bird changes from tone to noise. We thank our generous hosts who introduced us to the live, spontaneously singing males of *Otus atricapillus atricapillus*: J. C. and L. Magalhaes at Fazenda Barreiro Rico and N. Lopez-Kachalka at Cerro Corá. Behrstock and Marshall missed *O. sanctaecatarinae* and *O. hoyi* altogether—by hundreds of kilometers.

A welcome addition to the nightjar cassette is, at last, a trilled song for the Lesser Nighthawk (*Chordeiles acutipennis*), although it is not the long one uttered while perched. These are the only nightjars still unrepresented in voice archives: Rosenberg's Poorwill (*Nyctiphrynus rosenbergi*) of western Colombia and northern Ecuador, Salta Nightjar (*Caprimulgus saltarius*) of northwestern Argentina and adjacent Bolivia, White-winged Nightjar (*C. candicans*) of central Brazil and Paraguay, Cayenne Nightjar (*C. maculosus*) of French Guiana, Roraiman Nightjar (*C. whiteleyi*) of the Venezuelan tepuis, Sickle-winged Nightjar (*Eleothreptus anomalus*) of southeastern Brazil and northeastern Argentina, and the extinct Jamaican Pauraque (*Siphonorhis americana*) of Jamaica. Hardy (in litt.) has just learned that the White-winged Potoo (*Nyctibius leucopterus*) is rediscovered and taped near Manaus and that the song attributed to the Rufous Potoo (*N. bracteatus*) is probably a variant call of the Gray Potoo.

It is simple to judge relationships among nightjars because each species has one male advertising song. But with owls, on the second cassette, things get complicated because most species have two territorial songs, an A and a B, used in ritual duets of the pair. The female's voice is a third to a fifth higher in pitch than the male's and in some species is naturally harsh. That makes four songs per species for most Screech-Owls, with much, much more if we fool around with songs provoked by playback. By recording in stereo, you can sort out the antiphony of different sexes, adjacent pairs, and neighboring other species spacially. Yet Hardy et al. renounce this solution and have their stereo equipment neutered to mono for field use. But the safest way to tackle owl taxonomy is to stick to the pure, musical tones of the males. Several populations have no known "normal" song because they have been searched only by trolling with tape-recordings, which elicit gruff responses.

Although the owl cassette boasts recordings of all New World owls except the Peruvian species Maria Koepcke's Screech-Owl (*Otus koepckeae*) of Amazonas and Long-whiskered Owlet (*Xenoglaux loweryi*) of San Martín; still the A and B songs are not uniformly represented among the species of *Otus.* Let us note here which species on the cassette lack the unprovoked male songs suitable for comparisons:

Flammulated Owl (*Otus flammeolus*) from California. Normal (not bellicose) male, originally in stereo.

Eastern Screech-Owl (*O. asio*) from eastern United States. The lower-pitched songs are normal male A (whinny) and B (trill). Marshall's part originally in stereo.

Western Screech-Owl (*O. kennicottii*) from southeastern Colorado. Unprovoked pair duet of A (bouncing ball) but only the female's B (double trill). Originally in stereo.

Balsas Screech-Owl (*O. seductus*) from Colima. Harsh, provoked A (bouncing ball) song of female, then pair duet of B (double trills). Marshall's field notes mention mellow voices, but such spontaneous male songs have not yet been recorded on tape.

Pacific Screech-Owl *O. cooperi, lambi* race from Tehuantepec: Harsh, provoked A song of female followed by pair duet of B (double trills), mellow songs (Marshall, field notes) not yet recorded; nominate race from Guanacaste: Provoked pair duet, A. This taxon also has a double trill and mellow songs of the male (Marshall, field notes).

Whiskered Screech-Owl (*O. trichopsis*) from Miquihuana. Spontaneous A (trill) and B (Morse code) of male. Originally in stereo, impressive for the provoked calls during aggressive flight past microphone.

Tropical Screech-Owl (*O. choliba*) from Loreto. Unprovoked male's A (accented song) and B (short trill).

Peruvian Screech-Owl (*O. roboratus*) from Perú. Rapid, purring trills with prominent octave harmonic tone.

Bare-shanked Screech-Owl (*O. clarkii*) from Monteverde. Normal male songs A and B (Morse code) plus a female whine. All like *O. trichopsis* (Hardy in litt.), but slower.

Bridled Screech-Owl (*O. barbarus*) from San Cristóbal. Marshall has the spontaneous female, Behrstock the angry female response to play of "example 1."

Rufescent Screech-Owl (*O. ingens*) from Merida: Bouncing ball song, by an unprovoked male; from Ecuador: Same as the preceding except for less speed-up in the middle.

Cloud Forest Screech-Owl (*O. marshalli petersoni*) from Cajamarca. Normal male, higher-pitched than *watsonii.*

Tawny-bellied Screech-Owl (*O. watsonii*). Unprovoked male A songs: rapid trill from Taracoa, slow trill from Manu. Behrstock now has a B call, in Morse code, from La Selva Lodge, near Taracoa. An "A" trill of intermediate speed (3.7 notes/sec) is available from M. B. Robbins, proving that northern and southern populations are conspecific.

Variable Screech-Owl (*O. atricapillus atricapillus*) from São Paulo. Strident, highly outraged female, type A (long trill). All three of us have taped spontaneous, pure male tones A (trill) and B (bouncing ball) that are not on the cassette. A mellow female song is unknown in this population.

Long-tufted Screech-Owl (*O. sanctaecatarinae*) from Rio Grande do Sul. Harsh female A (trill) with mellow male A chiming in at the end. Both W. Belton and T. Parker have taped a normal male B (bouncing ball) that is not on the owl cassette. A mellow female song has never been heard.

Montane Forest Screech-Owl (*O. hoyi*) from Salta. Like the duet of *O. sanctaecatarinae*—a harsh female A with mellow male B (short, slow trill) answering farther off. R. Ridgely, R. Straneck, and König have all taped a very long, spontaneous male trill, not on the cassette. At only 11 notes per second, it is slower than the 13 or 14 notes per second usual for *O. atricapillus* and *O. sanctaecatarinae.*

Variable Screech-Owl (*O. atricapillus guatemalae*) from Nayarit and *O. a. napensis* from Huánuco. Spontaneous male A (long trill). The duetting female sings the same song about a fourth higher in pitch (Marshall, field notes) that has not been recorded on tape.

Vermiculated Screech-Owl (*Otus vermiculatus*) from Achiote Road. Spontaneous pair duet of incredibly short trills, setting a record for the genus.

Puerto Rican Screech-Owl (*O. nudipes*) from Ciales. Male A (mellow trill) followed by B (ghoulish duet of pair), all spontaneous and in antiphony with neighboring pairs. Originally in stereo.

Cuban Screech-Owl (*O. lawrencii*). Male unprovoked bouncing ball.

White-throated Screech-Owl (*O. albogularis*). Spontaneous pair duet of doublets. M. B. Robbins has available the even, A-type song, not on the cassette.

The brochure has a built-in propensity to create errors through the use of numbers keyed to species or vocal examples. We have convinced the authors of the cassettes to combine the numbered remarks with the species to which they refer; but the dangling example numbers are still to blame for transpositions such as these: Early versions of the owl brochure reversed the Manu and Taracoa *Otus watsonii*; in the current nightjar brochure, the order of examples for the Whip-poor-will (*Caprimulgus vociferus*) does not follow the cassette, which is first North Carolina, then New Jersey, and finally Michoacán for the gravel-voiced, southwestern form with pure white eggs. We suggest that the silver-throated maestro merely states the locality instead of reciting example numbers; for instance, "*Caprimulgus vociferus,* the Whip-poor-will, from North Carolina . . . from New Jersey . . . from Michoacán . . . ," as we have done above. That would protect the many recordists from having their precious vocalizations wind up in the wrong taxon. Getting rid of the abominable example numbers would make the tape free-standing and the system self-correcting.

The cassettes are the triumph of cooperation between professionals and amateurs, benefitting especially from expertise of scientific tour leaders. The tapes are a valuable link with the past. Indeed, when the forest is cleared, the marsh drained, and the prairie paved, the sounds of birds in their natural settings can—besides providing study material—lift the spirits and give hope in a way that no study skin or photograph can. Where the habitat still stands but travel is dangerous, the study of bird sounds from tapes continues in the absence of further observations. It is no coincidence that the two owls not represented by voice are from Perú, currently one of the most volatile countries in South America.

There are still many things nightbirds say that are not on these cassettes, besides the missing species and spontaneous male calls we listed. There are some grunts and howls of the Black-banded Owl (*Ciccaba huhula*) and deep groans of the White-chinned Owl (*Pulsatrix koeniswaldiana*) that are needed. The vocabulary of the Band-bellied Owl (*P. melanota*) remains virtually unknown. Also required are the loud, gruff barks of the Rufous-legged Owl (*Strix rufipes*) and the high, thin nest-begging pleas of the Unspotted Saw-whet Owl (*Aegolius ridgwayi*). The pygmy-owls seem ripe for splitting, and there may be an unnamed potoo (or two) out there. The Buff-fronted Owl (*Aegolius harrisi*) jumps from the paramo fringes of Colombia and Venezuela across Amazonia to the lowland forests of Misiones, Argentina. The vocabularies of its disjunct populations need a work-up comparable to that of the Boreal Owl (*Aegolius funereus*), studied by König. All these novelties await discovery by a cadre of amateur and professional naturalists who enjoy a quest, and who are not intimidated by snakes, mosquitoes, or things that go bump in the night.—Joe T. Marshall, Robert A. Behrstock, and Claus König.

Frontispiece.—Variable Screech-Owl (*Otus atricapillus*) and Its Relatives.

We use the term "*atricapillus* superspecies" for the group of taxa shown here. They are related closely, they occupy two continents, and they nowhere overlap in distribution. Morphological distinctions are few and individual variation is extreme. Irides are yellow except that Peruvian Sira, Paraguay, and São Paulo birds have a brown iris in the dark phase, yellow in the red phase. Tarsus of the holotype of *cassini* is not shown because feathering is the same as the birds to each side of it. Tip of tarsus is less feathered within Panamá and on either side of Panamá than elsewhere. Tarsal feathering becomes luxuriant from Bolivia south, covering base of toes. If you want to see the whole owl, just put a straight-edged mirror on the midline.

Color variation among all the specimens we examined, whose localities are shown as black dots on the map, follows this rule (Marshall, Monogr. W. Found. Vert. Zool. 1:1–72, 1967, p. 25): Individual variation is extreme in the central part of the geographic range and it includes a red phase; whereas, at the periphery, the red phase drops out, specimens are uniform, and the populations resemble each other. Thus the taxa in Sinaloa, Yucatán, Salta, and Rio Grande do Sul have the same coloration—tawny back with those little buff pagodas. This all frustrates the use of scientific names for color races so let's try a system based on the different kinds of male vocalizations shown. Triangles stand for the tape recordings we studied from the Library of Natural Sounds and from the Bioacoustic Archive, whose curators we thank. Red curves enclose areas whence tape recordings sound alike. We will recognize each of those areas as the home of a major taxon, listed from north to south as follows.

Variable Screech-Owl (*Otus atricapillus guatemalae*). We thank J. W. Hardy for suggesting this appropriate common name, better than our "Protean Screech-Owl." From west to east the recordings of the long trill are from San Blas, Nayarit by John Arvin; southwest corner of Durango, Comitán, and Xcan—all by Irby Davis; upper Sarapiqui, Costa Ricá by Gary Stiles, and Paramba, 3500 feet, Ecuador by R. S. Ridgely.

Vermiculated Screech-Owl (*Otus vermiculatus*). This identification is based on Behrstock's color photo on the jacket of "Voices of the New World Owls" by J. W. Hardy, Ben B. Coffey, Jr., and George B. Reynard (ARA Records, Gainesville, 1990), reviewed by us in this issue. The photograph was made while G. Clayton tape-recorded the same bird, the upper sonagram, on Achiote Road, Canal Zone. D. Engleman recorded the same pair. The other recorded songs, somewhat different from each other but all short, are from Barro Colorado by Marshall, Pipeline Road by L. Kibler, Isla Majé by P. Polchek, and Cerro Pirre by D. Engleman, the lower of the two short sonagrams.

Variable Screech-Owl (*Otus atricapillus roraimae*). This song was discovered by P. Schwartz in the 1960's and is recorded in great beauty and purity by S. Coats, who associates it with *vermiculatus*-like specimens. The high pitched song has the peculiar timbre and gradual descent in pitch evoking the Asian Barred Owlet (*Glaucidium cuculoides*) of Thailand. From north to south the tapes are from Colonia Tovar and Portachuelo Pass, Aragua, Venezuela, by P. Schwartz and S. Coats; Brownsberg Nature Park, Surinam, by Behrstock; and Jirilla, Perú by T. Schulenberg. The Surinam bird was recorded at 450 m altitude on two trips by Behrstock. He and D. Markley saw the bird well enough one late afternoon to be sure it was a Screech-Owl. This is a new species for the Surinam list.

Variable Screech-Owl (*Otus atricapillus atricapillus*). From central Peru south to São Paulo the tapes are a return to the long trill of México. These are, from west to east, Cerros del Sira, Perú by J. Weske; Cerro Corá, Paraguay by Behrstock and Marshall; Iguazú, Misiones, Argentina by M. Castelino, R. Straneck, and König; and Barreiro Rico, São Paulo by W. Belton, J. C. Magalhaes, Marshall, and Behrstock.

Long-tufted Screech-Owl (*Otus sanctaecatarinae*). From Rio Grande do Sul, Brazil, are tapes of a giant screech-owl whose unprovoked male utters two kinds of territorial calls, A (short trill) and B (bouncing ball), both shown at lower right. It was recorded throughout the state by W. Belton and at São Francisco de Paula by T. Parker.

Montane Forest Screech-Owl (*Otus hoyi*). This new form was tape-recorded at Salta, Argentina by R. Ridgely, R. Straneck, König, and B. Whitney. The unprovoked song sounds like *O. atricapillus atricapillus* but a sonagram shows it is slower; therefore it is left outside the red balloon along with a similar song from lowland Surinam (by B. Whitney). The specimens are uniform, except for a red morph, and look like miniature *Otus sanctaecatarinae* with short tufts.

SPECIAL REVIEW

A GUIDE TO THE BIRDS OF COSTA RICA. By F. Gary Stiles and Alexander F. Skutch. Cornell Univ. Press, Ithaca, New York. 1989:511 pp., 52 color plates by Dana Gardner, 39 photographs (mostly of habitats), 2 maps, 2 glossary diagrams. Hardcover $65.00, softcover $35.00.

A GUIDE TO THE BIRDS OF PANAMA (2nd ed.) WITH COSTA RICA, NICARAGUA, AND HONDURAS. by Robert S. Ridgely (author) and John A. Gwynne (artist). Princeton Univ. Press, Princeton, New Jersey. 1989:534 pp., 48 color plates, 61 black-and-white illustrations of birds (some of multiple species), 2 endpaper maps. Hardcover $49.50.—In recent years Costa Rica has become arguably the country most frequently visited by birders seeking an introduction to the avifauna of the Neotropics. In an area often compared to that of the state of West Virginia, some 830 bird species have been recorded, and the habitat diversity within such a small area, from cloud forests to ocean beaches, is amazing. Until recently, the only books that covered the birds of Costa Rica were the pioneering work of Carriker (1910) and the ecologically oriented monograph of Slud (1964), both of which are long out of date with reference to distribution, plus the ornithological portion, by Stiles and others, of the massive "Costa Rican Natural History" (Janzen 1983). The latter includes a useful (but already somewhat outdated) table of the abundance and habitat status of Costa Rican birds at eight localities, and accounts written by specialists, of 53 species (or groups as in the case of antbirds). These are arranged alphabetically and inconveniently by generic name (except, again, for the "Antbirds" segment), an editorial policy also followed in the portions on other animals and on plants.

None of these works was in any way a field guide. For identification purposes prior to 1989, birders usually relied on the Mexican guide by Peterson and Chalif (1973) which includes about two-thirds of the birds of Costa Rica, and the Panama guide by Ridgely (1976, with supplementary information added in the 1981 printing). I have not made a count, but I believe that illustrations of fewer than a half dozen Costa Rican species are missing from these combined books. There were, of course, few or no statements in either book on the distributional status of bird species within Costa Rica. I found myself checking the tables in Janzen (1983) or the status statements in Slud (1964) to determine whether a particular sighting was reasonable; this did not help much in the cases of some well-known North American migrants that were almost unknown in Costa Rica (e.g., *Tyrannus verticalis, Vireo griseus, Dendroica tigrina*).

It was known that a comprehensive book on Costa Rican birds by the two most appropriate authors, F. Gary Stiles and Alexander F. Skutch, was in progress during the early 1980s, but nobody seemed to have any firm idea as to when publication might be expected. The originally planned publisher, Ibis Press, eventually had to abandon the project. It was taken over by Cornell University Press where Robb Reavill, scientific editor, gave periodical progress reports; having birded in Costa Rica, she knew full well how much we needed the Stiles and Skutch book.

"Long awaited" is a cliché in book reviews, but it certainly fits "A Guide to the Birds of Costa Rica." Meanwhile, however, with much less publicity, Robert Ridgely was working on a major revision of his Panama guide, the text of which which allegedly was to be expanded to include the birds of Costa Rica, Nicaragua, and Honduras; these had been briefly listed in a 7-page appendix in the original edition. When the new version appeared, only weeks after the publication of the Stiles and Skutch book, we found that the geographic coverage had indeed been expanded.

A comparison of these two new books with respect to usefulness for birders in Costa Rica

obviously was in order. I was able to take both with me on my fourth visit to that country, 26 March to 6 April 1990, to make just such comparisons. I spent 27–29 March observing birds during my fourth stay at Hacienda Selva Verde on the Rio Sarapiqui in the Caribbean lowlands and 30 March–5 April at Tiskita Lodge, on Bahia Pavones, on the east side of the Golfo Dulce, Pacific lowlands, where many of the birds were new to me. Before taking up the matter of comparative usefulness as field guides, I will discuss the general formats of the two books. To save space, I will refer to Stiles and Skutch as S&S, and to Ridgely and Gwynne (the artist is given full coauthorship in this edition) as R&G.

Although its scope has indeed been extended north to Honduras, R&G is still basically a book on the birds of Panama. A 37-page appendix covers the 162 species of birds that have occurred in Costa Rica, Nicaragua, and Honduras, but not yet in Panama. Eight additional color plates figure 127 of these species, with eight more (including, oddly, Brown Creeper [*Certhia familiaris*], Eastern Bluebird [*Sialia sialis*], and Red-winged Blackbird [*Agelaius phoeniceus*]) shown in line drawings. The rest of the book is a major revision of the original "Guide to the Birds of Panama." A short introduction to the second edition is followed by an essentially unchanged chapter on "Climate" and an updated chapter on "Migration and local movements." The original chapter on "Conservation" is now expanded into an important 6-page chapter called "Recent developments in Panama ornithology and conservation." The chapter entitled "Plan of the book" is essentially the same in both editions, except that in the revision the classification and nomenclature are mostly those of the AOU Check-list (1983), so comments in the "Plan" cover the treatment of departures from names used in the first edition or in the AOU Check-list.

Absent from the first edition (and from S&S) is a nominal (English) checklist with columns for the four countries of southern Middle America, useful for marking off species seen in each country. I have used the Costa Rica column to indicate on which of my four visits I saw a given species, as a handy index to my field notes.

The appendix on "Finding Birds in Panama" has been enlarged and updated and is now credited to Dodge and Lorna Engleman as well as to Ridgely; Dodge Engleman was record-keeper for the Panama Audubon Society.

The second edition of R&G is 130 pages longer than the first edition, and this is not attributable solely to the new geographic coverage and the expanded chapters mentioned above. Since 1976, 46 species were added to the Panama list, necessitating new species accounts. In addition, many of the species accounts themselves have been substantially enlarged. To give but one example, while in Costa Rica in 1990, I had occasion to study the accounts of the three species of *Formicarius* that occur in Panama. In the first edition, these occupied 93 lines of type; in the second, 138 lines. The upshot is that for anyone planning to visit Panama, purchase of this book is vital, even though one may already own the first edition.

Comparisons between S&S and R&G can be made at two levels. First, how thoroughly do they serve as introductions to their respective countries, and second, how well do they serve for field identification in actual use? The coverage of geography, climate, and avian habitats in S&S for Costa Rica is much more detailed and comprehensive than the similar information for Panama in R&G. Maps in the latter are confined to the endpapers; in the front, a rather simple map of Panama showing political subdivisions, major roads, and some of the most frequently mentioned localities, and at the back an enlarged map centered on the Panama Canal. Neither map has a scale, and neither indicates altitude. In contrast, S&S includes three maps (with scales). The first shows geographical regions, major topographic features, and landforms of Costa Rica. The second shows provinces, cities, major towns, main highways, and protected areas (national parks, biological reserves, and wildlife

refuges). Numbered circles refer the reader to an appendix giving an annotated list of birding localities in Costa Rica, which is accompanied by the third map, of birding localities, towns, and major roads of the Valle Central, centered on the capital city of San José.

The introductory chapters include many photographs of avian habitats, another feature lacking in R&G. However, they suffer from the gray, low-contrast reproduction prevalent in so many recent books.

A useful additional feature is an "Illustrated glossary of anatomical terms used in the text," which goes well beyond the usual diagram found in many bird books. In addition to the descriptive terms identifying areas of the bird (12 for the bill region alone), there is an illustrated list of plumage patterns and markings as well as tail shapes. These should be helpful for beginning birders, and in some instances illustrate the authors' concept of relatively uncommon terms such as "half-hood" and "chevroned."

Both of the authors are long-time residents of Costa Rica (Stiles has since moved to Colombia), whereas Ridgely, master birder though he is, remains a visitor to Panama (as will be most of the users of his book). This is reflected in the depth of information presented in a 10-page introductory chapter on "The Costa Rican avifauna," which includes material on zoogeographic affinities, song, breeding, plumage and molt, movements, and food and foraging. Within the species accounts, S&S have separate paragraphs for voice and nest. In R&G, voice is often, but by no means always, described in the "habits" paragraph, and nesting is mentioned only in general terms in the short paragraph introducing each family. The family introductions are much longer in S&S, and the "habits" paragraph much more comprehensive, reflecting the particular interests of its authors.

Both books present taxonomic and nomenclatural notes where appropriate. This is useful, as the treatments of some taxa differ in the two (for example, in the Nightingale-Wren [*Microcerculus*] complex). English names are also sometimes discordant. Neither book has a table of contents such as that in the AOU Check-list, listing orders and families. However, thumbing through the pages devoted to the Passeriformes, it is clear that R&G fully adopt the sequence of the AOU, whereas S&S frequently depart from this sequence. Some of these departures, such as the reversal of sequence of the Furnariidae and Dendrocolaptidae, are not explained; in other instances, such as the novel arrangement within the Tyrannoidea (Tityridae, Cotingidae, Pipridae, Tyrannidae), have a few words of explanation. The components of the AOU's Emberizidae are given full family status, and their sequence rearranged (Coerebidae, Parulidae, Icteridae [including *Spiza*], Thraupidae, Emberizidae). The authors' preference for smaller families is mentioned under the family account for Emberizidae, but no explanation is given for their revised sequence of "9-primaried Oscines."

A comparison of the color plates by Gwynne (Panama) and Gardner (Costa Rica) obviously is in order. Neither artist is a Guy Tudor, although Gwynne pays homage to Tudor in some of his paintings, notably the flying macaws of plate 11 and the dust jacket, strongly reminiscent of Tudor's rendition in Meyer de Schauensee and Phelps (1978), which was a plate singled out by O'Neill (1979) for particular praise.

With a few exceptions (such as the trogons and the larger tanagers), the figures on Gardner's plates tend to be smaller and more crowded, sometimes severely so, than those of Gwynne. Similar crowding in Gwynne's plates was avoided for several groups by the addition of numerous black-and-white text figures, without counterpart in S&S. The format of Gardner's plates is essentially that of most field guides, with all of the birds facing the same way and in identical poses. Some of Gwynne's plates approach this format (hummingbirds, woodcreepers), but in most the figures vary more in pose and orientation. Most of Gwynne's birds thus look more alive and less stereotyped, with a possible loss in comparability. A few of Gardner's birds border on the grotesque, such as the goggle-eyed Common Potoo (*Nyctibius griseus*) of plate 51. Because of their stylistic individuality, the renditions of

individual species by the two artists are often markedly different; compare, for example, Gwynne's relatively lifelike night-herons on plate 2 of R&G with the stiff and badly proportioned versions by Gardner on plate 5 of S&S.

In some instances the subspecies found in Panama and portrayed in R&G differs noticeably from the Costa Rican subspecies. A good example is the Black-bellied Wren (*Thryothorus fasciatoventris*). Gwynne painted the subspecies *albigularis,* which occupies most of the Panamanian range of the species. It is conspicuously barred black and white on the posterior underparts. The Costa Rican subspecies *melanogaster* is much darker, and in the dense thickets favored by this species the posterior underparts appear solid black.

There are some unaccountable discrepancies between the two books in dealing with a given species. The R&G *description* of the juvenile Rufescent Tiger-Heron (*Tigrisoma lineatum*) is accurate, as are the description and plate in S&S. However, Gwynne's *figure* of this plumage (pl. 1, fig. 26b) does not match the description, nor does it look anything like the dozen or so skins I have examined. Both color and pattern are at fault. There is also a text discrepancy in this species; S&S state that *Tigrisoma lineatum* takes "at least 2 years to acquire adult plumage," whereas R&G indicate that this transition "requires about 5 years."

The plates in S&S are arranged in essentially natural groupings, with a few justifiable exceptions (tinamous and galliform birds share plate 12, for example). There are two additional plates at the end, of accidental, hypothetical, and recently added species. In R&G, a decision whose rationale escapes me has deemed that North American migrants be grouped together in their own plates rather than with their tropical relatives. Thus plate 31 contains migrant vireos and wood warblers, and the heterogeneous plate 32 includes the Gray Catbird (*Dumetella carolinensis*), the four migrant forest thrushes, a pair of Indigo Buntings (*Passerina cyanea*) and a pair of Rose-breasted Grosbeaks (*Pheucticus ludovicianus*), females of Blue Grosbeak (*Guiraca caerulea*), Bobolink (*Dolichonyx oryzivorus*) and Dickcissel, pairs of two migrant orioles and two migrant *Piranga* tanagers, the Acadian Flycatcher (*Empidonax virescens*) and Eastern Wood-Pewee (*Contopus virens*) (with the Tropical Wood-Pewee [*C. cinereus*] thrown in for comparison!). The flycatchers are thus seven or eight plates away from the tropical species with which they might be confused. Two plates are geographically segregated, which seems justified given the endemism at opposite ends of Panama. Plate 14 includes hummingbirds and furnariids largely confined to the Chiriqui region of western Panama (many of these occur in eastern Costa Rica as well), and plate 40 includes a miscellany of species known in Panama only from the east, particularly Darién.

The critical question for many readers will be whether the Stiles and Skutch book will suffice for field identification purposes—obviously it is vital for its general information about Costa Rica. Unfortunately its text is inferior to that of the Ridgely and Gwynne book for use as a field guide. The "Description" paragraph is in some instances inordinately long and detailed, especially for a figured species, but most critical is the lack of typographical highlighting of the critical characters for identification; the only eye-catchers are bold face for adult versus young or immature (apparently used interchangeably), and large and small capitals for seasonal plumages when appropriate, as in "WINTER" and "BREEDING" for the Rose-breasted Grosbeak (although it hardly needs to be pointed out that this species does not breed in Costa Rica). R&G emphasize with italics, in a relatively short descriptive paragraph, those characters critical for field identification, and follow this with a "Similar species" paragraph. Voice, however, is more consistently presented by S&S. That book also give details about distribution within Costa Rica; this is done adequately by R&G for the non-Panamanian species in the supplement, but not for species in the main text, where a broad general range statement ("Southern Mexico to northwestern Colombia") follows the detailed paragraph on the status and distribution of the species within Panama.

I have been told that Stiles never visited the southeasternmost corner of Costa Rica, at

least not beyond Golfito and the Rio Coto. This would explain a few vaguenesses about the status of birds in this corner of the country, which I visited in April 1990, and the erroneous statement that the Olivaceous Piculet (*Picumnus olivaceus*) does not occur in the Golfo Dulce region; that claim would come as a surprise to the piculet that was avidly tapping away within less than a hundred yards of my cabin at Tiskita! Ridgely attributes this species to "more humid lowlands and foothills on Pacific slope in Chiriqui," which is the area of Panama immediately adjacent to the east side of the Golfo Dulce, Costa Rica. Thus for the Golfo Dulce area, the Panama distribution statements may be more revealing than those given by Stiles and Skutch.

It is impossible to recommend, to visitors to Costa Rica, complete reliance on either of the books reviewed here. Try to fit both into your luggage. As a general reference book on Costa Rica and its birds, rather than as a field guide, the Stiles and Skutch book is irreplaceable. In contrast, in writing his guide to the birds of Panama, Ridgely was fortunate in that the four-volume work by Wetmore (1965–1984) is available as a general reference, and he could thus concentrate on field identification plus current status and distribution in Panama. Both books will be vital for years to come to anyone studying the birds of southern Middle America.

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SPECIAL CONSERVATION REVIEW
PARALLEL UNIVERSES: ENVIRONMENTAL PROPOSALS FOR THE 1990S

Conservation of Avian Diversity in North America. (Prepared by the Office of Migratory Bird Management, U.S. Fish and Wildlife Service, Washington, D.C., May 1990: 22 pp. Available from O.M.B.M., 634 ARLSQ, FWS, 1849 C St., N.W., Washington, D.C. 20240.)

Threatened, Endangered & Sensitive Species Recovery & Conservation: Action Plan, April 1990:14 pp. Available from D. F. Jolly, Southwestern Region, U.S.D.A. Forest Service, 517 Gold Avenue, S.W., Albuquerque, New Mexico 87102.)

A National Center for Integrating Ecological Research. (A report to the National Science Foundation on the results of a workshop organized by the Association of Ecosystems Research Centers, 1989:12 pp. Available from J. E. Hobbie, The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543.)

1990's Global Change Action Plan Utilizing a Network of Ecological Research Sites. (A proposal from sites conducting long-term ecological research workshop held November 1990, Denver, Colorado, 1990:36 pp. Available from the Long-Term Ecological Research Network Office, College of Forest Resources, AR-10, Univ. of Washington, Seattle, Washington 98195.)

National Institutes for the Environment: A Proposal. (Published by the Committee for the National Institutes for the Environment, 1990:8 pp. Available from N.I.E. Committee—Washington Office, 730 11th St., N.W., Washington, D.C. 20001-4521.)

Research Priorities for Conservation Biology. Edited by M. E. Soule and K. A. Kohm. (Published in cooperation with the Society for Conservation Biology.) Island Press, Washington, D.C., 1989:98 pp. $9.95 paper.—The last two years have not been kind to environmental scientists with limited reading time. The primary literature apparently doubles every few months, and now a new genre of publication has surfaced. The six "documents" listed above are probably not the only ones to have been produced of late; they are merely the ones that have reached my desk. All appear to be attempts to claim or protect turf and request funding. All were drafted before Iraq's invasion of Kuwait in August of 1990, as well as the more recent economic downturn, and all seem to be probing for part of the apocryphal "peace dividend" many believed would be available at the end of the Cold War. Indeed, one of the publications, the proposal to establish a National Institutes for the Environment, compares the potential and need for creating an N.I.E. at the end of the Cold War, with the establishment of N.I.H. at the conclusion of World War II.

Clearly, all six publications were written for educated lay audiences, not for conservation biologists, although all provide ample background information for anyone considering drafting a proposal of their own. Two of the publications, "A National Center for Integrating Ecological Research" and "1990's Global Change Action Plan . . . ," both of which result from N.S.F.-sponsored workshops, are slick, full-color presentations that are apparently direct descendants of the Super-Collider proposals, which proved so effective on Capitol Hill several years back. Ecology, thanks to desk-top publishing, is following closely on the heels of Big Science.

Although the six publications have much in common—all of them, for example show little evidence of the others' existence—each has its own agenda. The two agency publications summarize overly ambitious plans apparently designed to carve substantial niches for both agencies in the field of conservation biology. My only fear is that once carved, large portions of these niches will remain vacant for some time. For example, although fewer than half of the Federally Threatened or Endangered species occurring on land managed by the U.S.

Forest Service currently have recovery plans, the Forest Service's action plan projects that "about 90%" of all Threatened and Endangered species will be recovered within the next 50 years. This goal is especially fantastic when one recalls that the Service currently invests 90% of its T&E budget on only four of 174 currently listed species found on N.F.S. land.

The Fish and Wildlife Service's plan, drafted to "to comply with [federal] legislation," undertakes a similarly ambitious, albeit laudable, goal, i.e., ". . . to conserve avian diversity in North America." The Service aims to achieve this goal by "maintaining populations of *all native bird species* and their essential habitats at reasonable levels, preventing *any of these species* from having to be listed as Endangered or Threatened, and ensuring continued opportunities for people to enjoy these birds" (*emphases are mine*). But if past is prologue, the U.S. Fish and Wildlife Service's suggestion that it will be able to manage this effort seems, at best, to be overly optimistic. Indeed, the Service is currently unable, or unwilling, to fund appropriately research units that concentrate on nongame species. (For a sobering review of magnitude of related problems involved in implementing the Endangered Species Act of 1973 as of late 1988, see Endangered species: management improvements could enhance recovery program, U.S. General Accounting Office Publication GAO/RCED-89-5, Washington, D.C.) On a less ambitious note, the first of 15 objectives listed in Conservation of Avian Diversity in North America suggests that the Service will coordinate monitoring nongame bird populations while minimizing duplication of effort. But even this objective will be difficult to achieve, given current and proposed levels of funding. A chilling passage on collection permits signals stormy weather ahead for those of us involved in hands-on research. I quote it without further comment to alert those with interests in this area: "Collection permits will be reviewed to determine the cumulative impact of collection activities on nongame birds. The process for issuing permits and other activities potentially contributing to incidental take will be evaluated."

Perhaps the most ambitious and worthwhile of all of the publications it that from the Committee for the National Institutes for the Environment. S. P. Hubbell, H. Howe, and D. E. Blockstein are spearheading an effort designed to create an N.I.E. that would "set priorities, train necessary scientists to provide critical data, and sponsor mission-oriented research that will address the priority problems." Their goal is to create a federally funded entity that would have a proposed annual budget estimated at $500 million over the first 5 years of its existence. Although small by N.I.H. standards (i.e., an $7.8-billion appropriation for FY91), the amount is considerable when compared with funding currently allotted to N.S.F. (i.e., $2.3 billion for FY91). The National Academy of Sciences is about to initiate a Congressionally mandated $400,000 feasibility study of the concept. As envisioned by its proponents, N.I.E. would include five distinct institutes (Biotic Resources, Sustainable Resources, Ecosystem Management, Climate Change, and Human Environments), which would oversee the dispersion of funds for extramural research, as well as four intramural centers (a Library for the Environment, centers of Environmental Education and of Data Management and Risk Assessment, and a Grants Office).

Rereading the six documents listed above in rapid succession left me with the distinct impression that environmental scientists are simultaneously developing in a number of parallel universes. Unfortunately, just as their counterparts in the science-fiction literature, these parallel entities give every indication of being oblivious of each other's existence. Several of them are about to collide in a mad scramble for what is fast becoming a shrinking monetary resource. Although competition may be the American Way, the combatants would do well to follow again the example of Big Science: Let's step back and consider a more united front. Unless we do, I fear that arcane Congressional infighting will determine the winners and losers in all of this. As we are all too well aware, that selective force does not

necessarily produce the best outcome. The proposed National Institutes for the Environment, which provides the broadest agenda and base of support, might provide a starting point.—Keith L. Bildstein.

Current Ornithology, Vol. 7. By Dennis M. Power (ed.). Plenum Press, New York, New York, 1990:xiv + 388 pp., 36 numbered text figs., 40 tables, 4 appendices. $75.00— Vol. 7 of the Current Ornithology series contains eight chapters written by 14 authors from the United States, Sweden, USSR, Belgium, and Norway.

Chapter 1, "Population Declines in Migratory Birds in Eastern North America," by Robert A. Askins, James F. Lynch, and Russell Greenberg provides a clear and concise review of what we know and what we don't know about this problem. The chapter follows a logical progression of questions. What birds have shown declines? Where have the declines occurred? And finally, why have the declines occurred? Throughout, the authors point out gaps in our knowledge and problems in research design and survey methods that have made interpretation of the data difficult. The authors suggest ways of improving research methodologies, future research directions that are needed, and implications for conservation.

In Chapter 2, "Avian Energy Storage," by Charles R. Blem, the author reviews the research on energy storage that has been conducted since 1976 focusing specifically on internal energy storage. Birds store energy internally as carbohydrates, lipids, or proteins. For each form of energy storage, the author presents the advantages and disadvantages of the storage form and the extent that it is used by different species. The majority of the chapter focuses on different aspects of lipid storage. One section examines environmental controls of lipid reserves and proximate and ultimate factors that determine the size of the lipid reserves. Three sections examine sources of energy used during periods when birds require unusually high levels of energy, such as for egg production, growth, molting, and migration.

Chapter 3, "Survival Rates and Their Relationship to Life-History Traits in Some Common British Birds," by Andrew Dobson, examines how the enormous amount of banding data generated by amateur and professional ornithologists can be used to estimate annual survival rates, particularly of common species, and to monitor changes in survival rates. The chapter begins by comparing three methods of estimating survival rates (Lack's method, Haldane's method for incomplete data sets, Haldane's combined method) and the biases associated with each. A comparison is made among the three methods using actual and simulated data sets. In the latter half of the chapter, survival estimates are used to compare how factors such as body size and reproductive strategy are related to adult survival rates. Unfortunately, the author assumes the reader is familiar with the three methods of estimating survival rates. As a result, many terms are not adequately explained. For example, in Figure 1 some of the symbols used are not defined which I found frustrating when trying to decipher the figure.

Chapter 4, "Food Storing in Birds: An Evolutionary Perspective," by Hans Kallander and Henrik G. Smith, could be subtitled "everything you ever wanted to know about food storing but were afraid to ask." The authors provide a summary of food-storing behavior showing what families it occurs in, the seasons storage occurs, and the places where food is stored. An extensive list of references is included. The authors develop a general model describing when food-storing behavior should be beneficial in terms of either survival rates or reproductive rates and generate predictions about food-storing behavior from the model. This chapter would make an excellent instant lecture for an avian ecology or ornithology class.

Chapter 5, "Nonbreeding Social Organization in *Parus*," by Erik Matthysen reviews the

existing literature on non-breeding social organization within the genus *Parus,* discusses inter- and intra-specific variation in social behavior, and examines several hypotheses to explain this variation. A similar review by Jon Ekman appeared in the *Wilson Bull.* 101: 263–288. After reading both reviews and working with the Black-capped Chickadee (*Parus atricapillus*), I am convinced that too much time has been spent trying to pigeonhole species into discrete behavioral categories, and too little time has been given to examining how social behavior varies with habitat, food supply, and population density. Matthysen makes the important point that our understanding of how social behavior differs among populations has been hindered by a lack of operational definitions of terms such as flock, group, stable flock, exclusive flock, and compound flock just to name a few.

In Chapter 6, "Age-Specific Variation in Reproductive Performance of Birds," Bernt-Erik Saether examines age-specific variation in the reproductive performance of birds and hypotheses to explain these differences. He finds that, in general, adults breed earlier and lay larger clutches than juveniles. In addition, for females that are the same age, females with more experience do better than females with less experience. These observations are discussed in terms of life history strategies.

In an interesting chapter by Douglas Siegel-Causey and Sergei P. Kharitonov titled, "The Evolution of Coloniality," the authors examine colonial behavior within an evolutionary context. They begin by providing a review of bird taxa where colonial behavior occurs and describe species as either obligate or facultative colonial species. They attempt to sort out factors responsible for colony formation and maintenance dividing them into 1) causal factors—those responsible for the transition from solitary to colony nesting, 2) formation factors—those which promote a particular type of colonial breeding, and 3) maintenance factors or those which help maintain this behavior in a population. They conclude by outlining a hierarchy of stages in the development of coloniality.

Chapter 8, "The Ecology and Evolution of Extra-Pair Copulations in Birds," by David F. Westneat, Paul W. Sherman, and Martin L. Morton, explores the frequency and significance of extra-pair copulations (EPC) in birds. In the past, EPCs have been generally ignored in ecological analyses of social behavior. New techniques using genetic markers have shown not only that EPCs occur, but also that they often result in offspring. These authors examine the costs and benefits of EPCs to both males and females in different ecological settings. Information in this chapter should be included in any lecture on the ecology and evolution of mating systems.

Because of the variety of subject matter presented in this text, some chapters will undoubtedly appeal more to certain people than others. As a whole, the volume is excellent, and the extensive literature reviews provided at the end of each chapter make this valuable for anyone initiating a research study on one of the topics discussed. I recommend this volume and others in the series particularly for libraries and individuals teaching courses in avian ecology or ornithology.—Margaret C. Brittingham.

Save the Birds. For the World of Tomorrow. By A. W. Diamond, R. L. Schreiber, Walter Cronkite, and R. T. Peterson. A PRO NATUR Book, Houghton Mifflin Company, Boston, 384 pp., hundreds of color photographs and paintings, $39.95.—I have recently discovered this remarkable series of books, the most remarkable that I have seen during the past 50 years. "Save the Birds" has been published in 14 countries and in 10 languages.

The series owes its inception to Rudolf Schreiber of PRO NATUR in West Germany. The British edition was published in 1987 with authors Antony Diamond, David Attenborough, and Ian Prestt. The American edition was published in 1989, with authors Antony

Diamond, Rudolf Schreiber, Walter Cronkite, and Roger Tory Peterson. Peterson is, of course, the Dean of American ornithologists and everyone knows the name Walter Cronkite.

This 384-page book has literally hundreds of excellent color photographs and paintings. It discusses birds and their habitats in the "Earth's great ecosystems: from oceans and oceanic islands, to mountains and tropical rain forests, to arid lands and towns and cities," to "Save the Birds—we need them." to "One World for Men and Birds," to "Saving American Birdlife."

The book discusses Jackass Penguins, Ruddy-headed Geese, New Zealand Black Stilts, California Condors, birds-of-paradise, Hawaiian honeycreepers, and a hundred more.

Roger Tory Peterson wrote: "If we are to save the birds, we have to make as many people as possible aware of the threats to their survival. I can think of no better way of doing that than through the publication of "Save the Birds.' I have contributed my own time and effort to this book because I feel it is one of the most valuable conservation projects of our time. We must save the birds, and in saving them, we will save the earth." In the last analysis, that is what is at stake for mankind.

The obvious point here is that the book will serve as a magnificent encyclopedia, not only for anyone who is interested in birds and conservation, but also to any other group of people: to pro-choice and anti-abortion activists, to farmers and politicians, to businessmen and professors, and to missionaries and city dwellers. That is, to anyone who anticipates being alive in the year 2010.

"Save the Birds" is a remarkable publication triumph, and the price makes it a genuine bargain.—Andrew J. Berger.

Ornithology: An Ecological Approach. By John Faaborg. Prentice Hall, Inc., a Division of Simon and Schuster, Englewood Cliffs, New Jersey 07632. 1988:x + 470 pp., 269 numbered black-and-white figs., 11 numbered tables.—It is quite refreshing to find an ornithology text that is not simply a reprint/revision of an older edition. This well-written book is based, as the title states, on John Faaborg's extensive experience in studying the evolutionary ecology of birds. It is divided into 16 chapters arranged in five parts. Each chapter has a Suggested Readings section and there is an extensive reference section at the end of the book. The index combines subject, common name, and scientific name entries. I used this book for my undergraduate ornithology class, and this review reflects student opinions as well as my own.

Chapter 1 gives an all too brief overview of avian paleontology. Here Faaborg outlines the various theories as to the origin of birds but chooses not to take a stand "until more paleontological evidence is found. . . ." Some difficulty arises as Fig. 1.1 shows birds arising directly from the Thecodonts, while Fig. 1.3 shows three possible avenues of ascent; from Thecodonts, from Saurischian dinosaurs, and from the crocodilian line. This was confusing to my introductory students. Chapter 2 covers functional anatomy, synthesizing this book length topic into a mere 43 pages. The age-old debate resurfaces, should there be a separate text for ornithology labs or should it be combined into the lecture text? To me there is too much lab-related information to be included in a text for the lecture portion of the class. What Faaborg does cover is well done, but it seems superficial to me (e.g., Fig. 2.16 and 2.17). Chapter 3 on bird flight ends the first part and is an adequate coverage of the material. The subsection on flightlessness is very good at tying anatomy to evolutionary ecology.

Part 2, on the diversity of birds, is heavily oriented towards competition theory and, while Faaborg does acknowledge the recent debate, he concludes ". . . competitive interactions are a major force in determining the diversity of characteristics of the birds we see today." For an introductory text, Faaborg gives excellent coverage to modes of speciation, using the

standard examples found in many other books. (Why aren't Fig. 4.10 and its accompanying text referenced?) Neither the caption nor text explanation for Fig. 4.11 tell the reader what is going on. What do the numbers mean? I could figure it out since I had read Haffer's original paper many times. My introductory students had trouble here. Fig. 5.7 is completely uninterpretable without going back to the original paper. (What are the numbers above the bird drawings, and what do the letters in the figure represent?) Is all of this material suitable for the undergraduate student? For example, an entire page is devoted to presenting a phenogram of the Lari (Fig. 6.1) but is only referred to in a single sentence in the text. Moreover, the horizontal axis is not defined, leaving the reader only to guess as to the meaning. Chapter 7 presents an ecological survey of birds, and the approach is unique. Birds are grouped into ecologically similar species and are portrayed with line drawings in group specific figures. The trouble is that the criteria for grouping appears to vary with the figure. For example, Fig. 7.7 lumps the "aerial fish eaters" based on similar prey types. But Fig. 7.8 combines the "long-legged waders," based apparently only on leg length, since there are fish eaters and filter feeders in the same group? This approach is interesting in that it exposes the introductory student to the birds of the world but may confuse the student into thinking the pictures actually represent the same guild membership. Some of the line drawings of birds do need a little work (Fig. 7.22 vireo?).

Part 3, entitled "Strategies for Survival," starts with foraging behavior, territoriality, and optimal foraging theory, continues with survival strategies in extreme environments, and ends with an extensive treatment of migration. In the latter, it is surprising that, given the competition theory slant of the book, Cox's paper on the role of competition in the evolution of migration is ignored. Editorial problems continue in Part 3. What do the open and solid circles in Fig. 10.8 mean? Only by going to the original reference could I figure this out.

The next three chapters comprise Part 4 and summarize reproduction in birds with coverage given to anatomy and physiology; reproductive behavior, including song and nest topics; and a wonderful chapter on adaptive variation. The section on mating systems is current but in too much detail for the needs of a typical undergraduate.

Part 5 deals with birds and humans and covers the value of birds to man, field techniques, and avian management. The chapters are interesting and well written, but it is here that the editorial problems hit their zenith. In Fig. 14.1 what do the letters stand for? In Fig. 15.3, the vertical axis for the top half of the figure is not labeled, and neither axis is labeled for the plots on the bottom half of the figure. By going to the originally cited work, I was able to figure out this figure. My undergraduates were totally lost. Fig. 15.13 is a black-and-white photo of a bird wearing color bands and a FWS leg band. Which is which is up to the reader. Without going to the original paper, Fig. 15.15 is uninterpretable. What are those numbers? Table 16.1 needs a trip to the original to figure out that the numbers represent the number of territories or estimated pairs per 100 acres. I was also concerned that the totals in the original paper didn't match the totals in the book. Then I noticed that the Blue Jay was left out of the book table. Why? Why weren't the correct birds names used (towhee, hummingbird, meadowlark, etc.), and what do the boxes around selected entries mean?

The book layout leaves a lot to be desired. The pages are nearly 8½ × 11 in. and the text is arranged as a single column 5 in. block, leaving a 3 in. blank on the left side of each page. The five in. block makes reading difficult, and the 3 in. blank is simply a waste of paper. For ease in reading, I favor the double column approach used by, for example, R. L. Smith in the 4th edition of "Ecology and Field Biology."

In sum, the book offers a great deal of useful information for the reader. It uses a new approach that is refreshing, and it is well written. I was able to incorporate a great deal of new information into my ornithology class. However, much of the material is too advanced for a typical undergraduate student majoring in either biology or wildlife biology and the editorial problems are somewhat frustrating.—Robert C. Whitmore.

ON THE WING: THE LIFE OF BIRDS: FROM FEATHERS TO FLIGHT. By Bruce Brooks. Charles Scribner's Sons, New York. 1989:192 pp., numerous photographs. $40.00.—Before reading or discussing this book, one should take note of Brooks' introductory statement (p. xiv): "This book should not teach anyone to feel secure in a comprehensive knowledge about birds. It should teach us all to be delighted that we can never find out enough." What follows this introduction is not an ornithology text, nor is it in any way a reference work or book of instruction. It is a book meant to instill wonder, not knowledge.

Brooks does this with great gusto. The book is filled with anecdotes about the biology of birds: anatomy and physiology, primarily relating to flight; reproduction, including nesting and parenting; and a chapter on "Birds and Man: Whose World Is This?" This last chapter is somewhat different from the usual plea for conservation. Brooks makes the usual complaints about decimation from habitat destruction, hunting, and the illegal pet trade. He then points out at length the efficiency of birds in controlling agricultural pests, citing examples of avian responses to insect outbreaks, saving crops, and the quantity of weed seeds and rodents consumed by birds. An aside on the last page is about how an ovenbird (probably the Rufous Hornero [*Furnarius rufus*]) ended an epidemic of Chagas' disease. He also brings up the important role birds have played as inspiration, especially in music. He contends that, without birds, our lives would be poorer, not just for the loss of birds to watch and listen to, but for the absence of their effect on our other aesthetic pursuits.

As is typical of a companion book (to the Public Broadcasting System's television series *Nature*), "On the Wing" has a highly readable text illustrated with numerous high-quality, often spectacular, photographs. As is also typical of the genre, the text can be frustrating to an expert in the field because of inaccuracy due to oversimplification. One must realize that, in order to present information at a level comprehensible to the lay reader, an author must gloss over details and complexities to an extent that can leave the reader with the feeling that life is simple, straightforward, and well-understood. Unfortunately, this book goes beyond the usual level of inaccuracy. For example, Brooks states that there are about 8800 species of birds in the world, as compared to about 4000 species of mammals and 7500 species of all other vertebrates combined (p. 3). One must assume that he means amphibians and reptiles, since there are well over 100,000 species of fish. Later, when discussing nesting, Brooks includes Mourning Doves (*Zenaida macroura*) and hermit hummingbirds (*Phaethornis* spp.) among the passerines (p. 97, 107). These and other statements are not oversimplifications; they are simply incorrect.

Another difficulty that authors of natural history books must contend with is the temptation toward anthropomorphism, especially when discussing evolution or behavior. In his zeal to express the wonder of ornithology, Brooks doesn't even try to resist that temptation. As an example, in describing the use of hymenopteran nests by some birds, he states (p. 104), "In a few cases, this is because the insect builds a strong structure of mud or papier-mache and the bird envies its snugness." His descriptions of bird anatomy are far more teleological than can be excused as "writing for a lay audience." He regularly refers to evolved structures and behaviors as if the birds consciously decided to adopt them, with statements like (p. 5) "If *Archeopteryx* needed only to keep warm, why didn't he grow hair and the layer of fat that usually supplements a fur coat?" and (p. 82) "The upper leg renders a service to the foot, without which the bird would never be able to relax on a perch." While it can be difficult at times to express evolutionary results without sounding a bit teleological, Brooks has gone beyond that degree, and the book's credibility suffers as a result. The PBS *Nature* series has a deservedly high reputation for quality, in its subject matter, its photography, and its scripts. While its anecdotes are certainly interesting and informative, this book does not live up to the standards set by other segments of that series.—ROBIN K. PANZA.

A Guide to the Birds of Puerto Rico and the Virgin Islands. By Herbert A. Raffaele, illus. by Cindy J. House and John Wiessinger, with single plates by Cynthie Fisher, Alejandro Grajal, and John Yrizarry. Princeton Univ. Press, Princeton, New Jersey. 1989:253 pp., 18 black-and-white and 24 color plates with caption figs., 9 location maps, 3 tables. Cloth, $39.50; paper, $15.95.—The first edition of this field guide fulfilled an important need for students of the birds of Puerto Rico and the Virgin Islands and was generally recognized as an important and well-written volume. The current version corrects some oversights of the first edition and updates the text to include new records obtained in the seven years since first publication. Plate to text cross-referencing, added in the new edition, eliminates the time-consuming and annoying searches from text to figures that were a drawback of the first edition. Eleven new bird species that have been recently documented from the region are added, bringing the total number of living species described in the text to 284.

One principal virtue of this guide is the collection of information on identification, distribution, biogeography, and conservation in a single volume, along with practical hints on field hazards, where to see birds, and how to get there to see them. Raffaele has designed his field guide with both the full-time ornithologist and the casual birding tourist in mind. The section on good places to find birds is extremely valuable for the visitor who is trying to fit some birding into his vacation or business trip and wants to see as much as possible. The technical information contained in the guide is very detailed and summarized in introductory sections to give the reader a clear overview of the regional avifauna. The section on conservation is based on long experience with the agencies involved and is particularly perceptive; policy makers would do well to heed the cautions raised about development and tourism in the region.

Species accounts are clear and often contain summaries of results from detailed or long-term studies of resident species. For example, we learn that Puerto Rican Todies (*Todus mexicanus*) are common forest birds, difficult to see but easy to hear, forage for insects by hover-gleaning from the undersurfaces of leaves, forage near the ground, catch an average of 1.8 insects per minute, are most active on sunny mornings after rain, and are misnamed. We also are told that they can be attracted by knocking two stones together, although this reviewer has yet to find the right two stones.

The plates are good quality and present the important field marks of each species clearly. All species described in the text are illustrated, making it unnecessary to carry other guides. Facing descriptions emphasize useful field marks and note the size of each species. Species that are widespread and contained in standard North American field guides are illustrated in black and white, but some difficult groups (e.g., small shorebirds and fall plumage warblers) are shown in color to aid identification. Species breeding in Puerto Rico and the Virgin Islands all are illustrated in color except for goatsuckers and swifts. My only complaint about the illustrations is the lack of the artist's signature on several plates.

The paper version of the previous edition (published by another press) tended to lose pages after a short time. This problem has been remedied in the new edition, and neither my hard cover nor paper copies show any signs of loosening pages, even after several months of hard use. Given the large difference in price, most people will probably prefer the paper version.

This work is an important contribution to the ornithology of the West Indies and certainly belongs in the library of any ornithologist with even a casual interest in the region. The wealth of heretofore unpublished information on the natural history of the birds of the area makes this volume a useful reference as well as an excellent field guide. Supplemental material gives a clear view of the regional avifauna and the relationships among resident, migrant, transient, vagrant, and exotic species. Most of all, however, this is the most current and

best produced of any of the field guides devoted to the West Indian islands. I therefore recommend this book for anyone who plans to spend any time in the region covered.—Robert B. Waide.

Connecticut Birds. By Joseph D. Zeranski and Thomas R. Baptist, illus. by Sheila McMahon. Univ. Press of New England, Hanover, New Hampshire, and London, England. 1990:328 pp., 4 maps. $35.00.—The daunting task of synthesizing over 75 years of literature and field observations has been undertaken in this volume, the first comprehensive review of Connecticut ornithology since 1913. The book begins with a historical overview of bird studies in Connecticut. Following sections deal with the ecological zonation of the state and the history of habitat changes. Species accounts are next and consist of reports on present and historic status, distributions, subspecies, and authors' comments. For uncommon breeders, nesting records are also included. The book concludes with three appendices (hypothetical and escaped species, places to watch birds, a checklist of Connecticut birds) and a bibliography of Connecticut ornithology.

Any regional compilation is a monumental task, but one for an area as heavily worked as Connecticut approaches impossibility, especially in terms of ferreting out all available data. Despite the problems involved, the authors have successfully produced a coherent view of the present and historic occurrence of birds in the state. There are inevitably some errors and missed records, but such lapses are few.

My principal difficulties with the text involved its weak coverage of quantitative population phenomena and habitat affinities. Existing data bases (e.g., Breeding Bird Surveys, Christmas Counts, Mid-winter Waterfowl Surveys) could have greatly improved assessments of population trends and current abundance which, as reported in the text were largely subjective assessments. Furthermore, available syntheses of population data were in some instances not well covered. For example, although the authors described populations of Black-capped Chickadees (*Parus atricapillus*) as not significantly changing in historic times, Loery and Nichols (Ecology 66:1195–1203, 1985) reported a substantial drop in chickadee populations when Tufted Titmice (*P. bicolor*) first invaded northwestern Connecticut. Other notable but unreported population phenomena are that in mixed conifer-hardwood forest in northeastern Connecticut, breeding Red-breasted Nuthatches (*Sitta canadensis*) outnumber White-breasted Nuthatches (*S. carolinensis*), at least in some years; Tufted Titmice are relatively rare; and Ovenbirds (*Seiurus aurocapillus*) are frequently the most abundant breeders (Craig, Conn. Warb. 7:27–31, 1987).

I was also disappointed in the limited discussion of morphological variation in Connecticut birds. For example, the weak sexual dimorphism of Connecticut White-breasted Nutchatches was not mentioned. Furthermore, despite an extensive literature on hybridization and introgression in northeastern populations of Blue-winged (*Vermivora pinus*) and Golden-winged warblers (*V. chrysoptera*), only the traditionally recognized hybrids of these species are listed in the text.

With respect to the principal thrust of the volume, the status and distributions of individual species, I found the authors' assessments generally very reasonable despite their subjectiveness. Documentation of rarities was particularly thorough. In certain instances, however, because there was little population quantification, I found assertions about status without substantiation. For example, no evidence presented leads to the conclusion that Ruby-throated Hummingbirds (*Archilochus colubris*) are declining. In addition, the commonness of some breeding species such as the Canada Warbler (*Wilsonia canadensis*) was underrated. In the hardwood forests of northern Connecticut it is actually common and widespread,

and scattered pairs breed to the coast even in eastern Connecticut. Yellow-rumped Warblers (*Dendroica coronota*), although reported as rare breeders, have proven to be widespread in northern and portions of southeastern Connecticut at least since the 1970s. Similarly, Virginia Rails (*Rallus limicola*), described as breeding uncommonly inland to fairly commonly along the Connecticut River, actually breed abundantly in brackish cattail marshes along the river, and pairs may be found in many small and shrubby wetlands in northern Connecticut.

Other lesser concerns include the format for literature citations. In places, author and date were cited, in others only the author was referenced, and in still others only the periodical was cited. The bibliography of Connecticut birds also appeared sparse. Some key references from the state bird journal, *The Connecticut Warbler,* were perplexingly omitted.

Despite its several shortcomings, I found the book to be a significant accomplishment for Connecticut ornithology. The review of historic records is impressively thorough, and it is this historical review that comprises the book's most important contribution. The book is also well-written, well-edited, and makes for quite interesting reading. It is an essential volume for students of Connecticut birdlife, and it will be a standard reference on Connecticut's avifauna for many years to come.—Robert J. Craig.

Habitat Management for Migrating and Wintering Waterfowl in North America. Edited by Loren M. Smith, Roger L. Pederson, and Richard M. Kaminski. Texas Tech. Univ. Press, Lubbock. 1989:xii + 560 pp., 4 color and 59 black-and-white photos, 89 figs. and 96 tables. $25.00 (cloth), $20.00 (paper).—This book is a collection of 20 commissioned review papers by over 60 knowledgeable authors on the management of migration and wintering habitats for waterfowl in the United States and Mexico. The title is slightly misleading as the book does not cover Canada, except for a small superficial look at British Columbia, and excludes Alaska.

Each paper describes and quantifies major migrating and wintering waterfowl habitats in the area it covers, stressing their importance and relative use by waterfowl. Other topics covered include wintering strategies of waterfowl, management techniques, importance of agricultural areas as a source of food for wintering waterfowl, mortality due to diseases, threats by environmental contaminants, nutritive value of foods, habitat loss, threats to wintering habitats, and research needs. The breadth and coverage of these topics varies between papers, but overall they provide a good overview.

The papers are grouped by flyways. Five habitats and/or regions are covered in the Atlantic flyway chapter: the tidal and nontidal wetlands of the northern Atlantic States, the Chesapeake Bay and North Carolina sounds, the south Atlantic coastal wetlands, the southern reservoirs and lakes, and the beaver pond wetlands. The Mississippi flyway chapter includes papers on Great Lakes marshes, riverine, and deepwater habitats for diving ducks, upper Mississippi valley wetlands, Mississippi alluvial valley and southern coastal marshes and lakes. The central flyway chapter has six papers: the northern great plains, high plains reservoirs and sloughs, playa lakes, rice prairies, Texas coast, and the east coast of Mexico. The Pacific flyway is covered by four papers: northwest riverine and Pacific coast, great basin marshes, central Imperial and Coachella valleys of California, and the Pacific coast of Mexico. The book concludes with a paper on the biopolitical strategies for waterfowl habitat preservation and enhancement.

As expected from such a wide geographical review, details of management techniques are lacking, but the papers provide a good source of reference, consolidating and summarizing published and unpublished literature up to 1989. The greatest value of the book is in its global view of the topic, which highlights similarities and differences throughout the wintering range.

The coverage is heavily biased toward the management of geese and dabbling ducks, reflecting in part the lack of information on wintering diving ducks, especially seaducks, but also their lesser economic importance. With a few exceptions, waterfowl population estimates are presented without any measure of precision and/or accuracy, which reduces the value of the information. I was annoyed a few times by the use of name abbreviations such as SAV for submerged aquatic vegetation, as I had difficulty finding some definitions.

The large number of figures and black-and-white photographs make the book easy and enjoyable to read. The style is surprisingly uniform, given the number of different authors.

I found the book interesting and informative. It provides a good overview of the diversity of wintering waterfowl habitats, wintering waterfowl ecology, and management strategies used in the United States and Mexico. It identifies research areas and consolidates a wealth of information on waterfowl management techniques. I strongly recommend it to anyone interested in waterfowl management and research.—Jean-Pierre L. Savard.

Flight Strategies of Migrating Hawks. By Paul Kerlinger. Univ. of Chicago Press, Chicago, Illinois, 1989:xv + 375 pp., numerous figures and tables in text, two appendices, $19.95 (paper), $60.00 (cloth).—This book is the culmination of almost 10 years of research by the author, who is the outstanding investigator of hawk migration of the decade. There are 13 chapters: ecology and geography of hawk migration, methods of study, natural selection, atomspheric structure, flight mechanics (theory and empirical observations), factors influencing flight direction, altitude of flight, flocking behavior, water crossing behavior, flight distances and strategies, and a conclusion. The appendices list 133 species of Falconiformes in categories of migration distance, water crossing during migration, flocking behavior, tendency to follow insect swarms, and which age or sex precedes the other in migration. The book is intended for both the professional and the amateur "who will take the time to think about the material." I fear that some sections of the book will confuse all but a few professionals and that the average reader will skip too many sections, or perhaps even worse, accept statements of the author uncritically. At times even Kerlinger appears confused; I present two examples. In the summary of his chapter on the influence of wind topography and geography on flight direction (p. 183) he states: "An alternative means of studying orientation behavior, proposed by Alerstam and others, incorporates partial drift, prevailing winds, and overcompensation. The resulting flight between breeding and non-breeding ranges is a curved line, ellipse or loop migration." These are hypotheses or models, not methods of study. The concepts in the first sentence do not lead to those in the second; indeed, overcompensation would tend to preclude loop migration. In his section on circling performance and turning radius within thermals (p. 150) he states: "Measurements of soaring performance of pelicans and Black Vultures, species with different aspect ratios but similar wing loadings, showed that the pelicans have similar turning envelopes (table 6.5). This means that in addition to wing loading, wing shape is important for determining soaring performance (turning envelope)."

The book is more of a personal statement than a dispassionate summary of our current knowledge of hawk migration. My prejudices are often the opposite of Kerlinger's biases, and I think a reader should be aware that his versions of several controversies may not be the best. For example, Kerlinger has a very low opinion of hawk counts, allowing only that they have value for such "nonscientific uses" as monitoring population fluctuations. He believes that the analysis of hawk counts, e.g., in respect to wind conditions, . . . "tell us little about migration strategies, especially flight behavior." Are his direct observations of flight behavior so vastly superior? Kerlinger et al. (Can. J. Zool. 63:755–761, 1985) tracked with radar 35 Sharp-shinned Hawks (*Accipiter striatus*) soaring and climbing in thermals. The tracks deviated a mean of 66° to the right of downwind, a remarkable performance

because this means that they moved 2.25 m perpendicular to the wind for every meter that they drifted downwind within the thermal. The high mean climb rate (2.7 ms^{-1}) indicates that the birds were in the central core of the thermal during their mean of 54 s of soaring. Kerlinger does not give the mean wind velocity; a reasonable estimate for diurnal wind 750 m altitude at Berne in September and October is 10 ms^{-1}. At this wind speed, a hawk would move 540 m downwind with the drifting thermal and 1213 m perpendicular to the wind within the core of the thermal. This leads to an impossibly large average thermal size, probably by a factor of three or more, even if we assume that all hawks somehow entered and left the thermals at the extremes of the diameter perpendicular to the wind. Obviously, something is wrong with these calculations, and it gives me pause about the accuracy of all of the radar data.

Kerlinger uses his observations of hawks flying between thermals to evaluate the effects of wind direction on flight direction. For observations of Sharp-shins at Woodbine, 36 km NNE of Cape May, New Jersey, Kerlinger and Gauthreaux (Anim. Behav. 32:1021–1028, 1984), he used: (1) a simple linear regression of wind direction on flight tract direction, a calculation that ignores wind velocity completely. He used the daily mean of flight direction for the regression, thus reducing the data to 15 points, with all days equal regardless of the number of tracks (a peculiar grouping of data that he used in no other analysis in any of his papers) and (2) he sorted all tracks into those occurring on either west, east or calm winds and calculated the mean track direction and again ignoring wind velocity. For observations at Berne he regressed flight directions on the wind components perpendicular to the PAM (principal axis of migration, basically the direction the birds prefer to fly). This is a method superior to the other two but its accuracy hinges on the estimate of the PAM. Kerlinger's estimate of the PAM for sharp-shins is based on recoveries of birds banded at Cape May, a distribution that has been constrained by the Atlantic Coastline and other geographic features, and, arguably, by wind drift. He then uses this PAM to evaluate the effects of wind and geography on individual flight paths. The logic of this method is elusive. Kerlinger concluded that there was no evidence for drift at Woodbine but that compensation for drift was incomplete at Berne. The disagreement between sites may be the result of differences in analysis, sampling error, or a real difference between localities. A simple analysis of hawks counted, using a method similar to (2), above, also yielded no relationship between wind direction and migration and thus no evidence for wind drift at Cape May during the sampling period, a fact mentioned only in passing by Kerlinger. At least in this case, the direct methods of Kerlinger appear to be almost as indirect, and require as much interpretation, as the indirect methods of using counts and do not appear to provide different or less equivocal results.

The chapter on the influence of wind and topography on flight direction is largely an overzealous effort to disprove the wind drift hypothesis and is a good example of Kerlinger's biased presentation. He characterizes recoveries of banded birds as "a neglected source of data," but he dismisses the suggestion of Mueller and Berger (Wilson Bull. 79:397–415, 1967) that recoveries of Sharp-shinned Hawks banded at Cedar Grove show evidence of wind drift because their sample is small, particularly if age and sex classes are considered separately. There are no significant sex or age differences in the geographic distribution of band recoveries in any sample, including the large sample of Clark (Proc. Hawk Migration Conf. IV, 1985) from Cape May, New Jersey. My calculations show that 16 of 17 sharp-shins banded at Cedar Grove and recovered in the next six months north of 35°N were east of 88°W, the longitude of Cedar Grove, but only 10 of sixteen recoveries south of 35°N were east of 88°W (Fisher exact $P = 0.0319$). This small sample is confirmed by another of birds banded at Duluth, Minnesota, 92°W longitude (Evans and Rosenfield, Inst. Council for Bird Preservation, Tech. Publ. No. 5, 1985). Fourteen of 16 birds recovered in fall or winter

north of 35°N were east of 92°W but only eight of 22 birds recovered south of 35°N were east of 92°W ($\chi^2 = 7.95$, $P < 0.01$). The geographic distribution of these recoveries agrees with the distribution of the direction of prevailing winds and I interpret this as evidence of wind drift.

Kerlinger concurs with Clark (1985) in arguing that wind drift cannot explain the concentrations of sharp-shins at Cape May because there are too few summer recoveries of banded birds to the northwest. The southeasternmost of the multiple ridges of the Appalachian Mountains lies only 150 km to the northwest of Cape May. The wind drift hypothesis predicts that few hawks would cross these ridges onto the coastal plain, and I would expect that the birds occurring at Cape May would be comprised almost entirely of the many birds breeding in Maine, New Brunswick, and Nova Scotia that would seem to have little choice but to migrate along the coast. It is thus surprising that five of 16 summer band recoveries are from localities north and west of the mountains. Indeed, the westernmost recovery is only about 180 km northeast of the eastern end of Lake Ontario; hawks breeding west of here are likely to be diverted westward by the Great Lakes, and probably as far west as Michigan, before continuing southward.

Kerlinger used the winter recoveries of sharp-shins banded at Cape May for his estimate of the PAM. Any user of any data from Cape May should consider the following: (1) Most sharp-shins at Cape May are young of the year (the age ratio of birds trapped at Cape May is 22.3 juveniles to each adult, compared to only, e.g., 1.3:1 at Cedar Grove. (2) *One third* of the winter recoveries of birds banded at Cape May are from localities *north* of the latitude of Cape May. (3) Two (2.7%) of the winter recoveries south of Cape May are from Bermuda! Few birds that are lost at sea will find their way to Bermuda, and it is thus likely that more than a small fraction of the sharp-shins that attempt to cross Delaware Bay end up dead in the ocean.

I believe that the key to the explanation of the above observations is as follows: adults have a specific goal, the locality where they spent the previous winter. Young birds lack a specific goal, are inexperienced, have a less well-defined migratory direction, are more likely to be led astray by adversely oriented leading lines and wind drift, are more likely to become lost on the peninsula of southern New Jersey, finally ending up at Cape May. Migration through Cape May thus appears to be maladaptive but obviously not so much so that the tendency for young birds to become lost there has been reduced appreciably by selection. Nothing in Kerlinger's book agrees with this hypothesis.

I have been extravagant in my demonstration of Kerlinger's excessive zeal for his ideas and the resulting bias in the book. I disagree with many other interpretations of Kerlinger but I found reading this book a very useful and stimulating experience. I highly recommend the book to all persons, professional and amateur, who have a serious interest in either migration or diurnal raptors. It should be read, thought about, and effort should be made to understand difficult material. It is the best summary of a variety of aspects of hawk migration available, and I expect it to retain this distinction for some time.—Helmut C. Mueller.

Evolutionary Dynamics of a Natural Population: The Large Cactus Finch of the Galápagos. By B. Rosemary Grant and Peter R. Grant. University of Chicago Press, Chicago, Illinois. 1989:350 + xix pp., 12 color plates, 96 figs., 71 tables. $65.00 ($24.95, paper).—Long-term studies of populations of marked individuals, begun in the 1960s and 1970s, make ideal subjects for monographic treatment. The Grants began their investigation of the Large Cactus Finch (*Geospiza conirostris*) on Isla Genovesa (Tower) in 1978 and ended it in 1988. Their focus was variation because variation is what they found. With

regard to bill dimensions, some Ground Finches (*Geospiza* spp.) are more variable than finches from North and Central America and on other island groups, and *G. conirostris* is the most variable of all. In addition, the bill of young birds is dimorphic in color, some pink, others yellow. Furthermore, male *conirostris* can be distinguished as A-males or B-males on the basis of song type. Variation is enhanced by hybridization, as evidenced by birds with intermediate dimensions and inappropriate songs. Several mixed pairings in fact were observed, one with a Sharp-beaked Ground Finch (*G. difficilis*) and two with Large Ground Finches (*G. magnirostris*) (about 1–3% of all pairings).

Not only are the birds variable, but the climate can be extraordinarily variable. Although generally less than 200 mm, rainfall can vary from zero (in 1985) to about 2400 mm from December to July (1982–1983, an El Niño year). Differences in temperature from year to year are "detectable but moderate." As P. R. Grant and his colleagues have shown earlier, and again here, the El Niño rains have tremendous impact on vegetation, flowering, and fruit and seed production.

The climatic regime imposes variation on survivorship and reproduction. Cohorts differ in annual survivorship and life expectancy. Survivorship and reproduction are generally high in wet years and low in dry years. After a drought, survivorship can be high because of low density. Males of the 1976 cohort survived an average of 4.3 years after their second year, whereas in five other cohorts they averaged 1.6 years beyond their second year. Number of fledglings per pair varied from none in 1985, when no breeding occurred, to 9.9 in 1987. Lifetime reproductive success varied greatly, as in other species, but success was dependent on the year in which an individual hatched. The most successful female bred in nine seasons and produced at least 110 eggs and 58 fledglings, whereas median lifetime reproduction of breeders was only 11 eggs and 6 fledglings.

As in most studies of this kind, data are analyzed in every way imaginable. I was overwhelmed with analysis after analysis, graph after graph, table after table. There is something for everyone. Everyone, that is, except me. I happen to be interested in long-term average values for survivorship, clutch size, age of first breeding, and number of clutches laid and broods reared per female. In focusing on detailed comparisons between cohorts, morph types, age groups, and so on with regard to their responses to a variable environment, the Grants do not make most of these values readily available or even calculable. But, this is characteristic of the genre. I have not found all of these data in *any* long-term study, even though the authors must have the data. I am hopeful that by my raising this point, investigators making long-term studies will calculate and report their long-term average values, as well as their detailed comparisons.

What I found interesting were several of the Grants' conclusions and observations. For example, that the major source of new alleles in the *conirostris* population on Genovesa is hybridization with *magnirostris* and *difficilis*. Including putative hybrids in the sample of breeding birds increased the coefficient of variation of bill dimensions by 20% and the variance by 35%. Hybrids, however, had short lives and were relatively unsuccessful. Second, that *conirostris* is so dependent on *Opuntia* on Genovesa that extinction of *Opuntia* (from, say, a pathogen) would result in extinction of *conirostris*. Third, particularly fascinating, that in the first year of the study A males and B males, distinguished by their songs, differed in bill length, diets, and foraging behavior. Breeding males with the same song type did not occupy adjacent territories. Could this be a case of incipient sympatric speciation? Alas, no. These differences did not persist.

This book reports a careful and detailed study of the effects of environmental variation on morphological, ecological, and behavioral variation of a species. I can recommend it without reservation.—Bertram G. Murray, Jr.

A Parrot Without a Name. By Don Stap. Alfred A. Knopf, New York. 1990:230 pp. $19.95.—Stap does an admirable job of introducing the reader to the Peruvian rain forest. His vehicle is the documentation of his experiences during expeditions to Peru with John P. O'Neill and Ted Parker of Louisiana State University. Because of his numerous collecting expeditions to Peru since 1963, O'Neill has catapulted LSU to the forefront of Neotropical ornithology. In recent ornithological literature, the descriptions of several new species from South America have been published. Invariably, O'Neill's name has been associated with them. A recent issue of the *Wilson Bulletin,* for instance, contains a paper on the distribution and systematic status of a screech-owl from northern Peru, and sure enough, O'Neill's name appears in the acknowledgments.

The expedition's destination, the Cordillera Divisor, is a small isolated outlier of the Andes near the Brazilian border where O'Neill had earlier discovered several birds new to science. The party of 15 persons, plus an additional 1500 pounds of equipment, traveled slowly upriver by dugout. Progress was frequently hindered by logjams, shallow water, or simple misfortune. After several days, the group was at last entirely cut off from civilization, immersed in the wild, unspoiled beauty of the Amazon rain forest. Anticipation ran high: at any time, the party knew that there was the real possibility of discovering a species never before known to the outside world. But O'Neill and his younger associate, Ted Parker, were painfully aware that even though this region encompassed one of the last truly wild stretches of Peru, they must work quickly, for a transcontinental highway was soon to be built through it.

Obviously, birds are what this book is all about—tropical birds. Avian systematics, distribution and behavior are the major chords, but the author also strikes occasional minor ones as well: species diversity of plants and insects in the jungle, for example. A discussion of the very real danger of the two poisonous snakes found there is another case in point. Some large mammals were encountered on the expedition, including several species of monkeys, a tapir (*Tapirus terrestris*), a capybara (*Hydrochoerus hydrochaeris*), and two jaguars (*Felis onca*). However, I was surprised to find not a single mention of any crocodilian! Nor is geography neglected, as Stap ties together the importance of the Andes and the mighty Amazon River system in controlling continental weather patterns. Woven throughout the book are lessons in conservation such as the consequences of human "progress" and our startling lack of knowledge about the biota of areas that are being decimated at an alarming rate.

This delightful narrative, a real adventure in tropical biology, will be required reading for my ornithology students. It is a well-written, timely plea for preservation of the remaining rain forest before there is none left to preserve.—Jack D. Tyler.

Biology of the Eared Grebe and Wilson's Phalarope in the Nonbreeding Season: A Study of Adaptations to Saline Lakes. By Joseph R. Jehl, Jr. Studies in Avian Biology No. 12, Cooper Ornithological Society, 1988:74 pp., 39 numbered text figs., 10 tables, 3 appendices. $14.00.—Those of us involved in studies of breeding birds often forget that there are another nine months of the year during which individuals of our study species have to engage in the unending "quest for survival." In some ways, this is a more tractable period for studying avian adaptations, since in most species it is not complicated by the compromises a nesting bird must constantly make between questions concerning reproductive fitness and those concerning survival. Jehl's studies of the phenomenal molt migrations and concentrations of Eared Grebes (*Podiceps nigricollis*) and Wilson's Phalarope (*Phalaropus tricolor*) are a case in point. During migration, large flocks of these two species

sometimes build up in highly saline lakes, where they exploit temporarily abundant food resources. By mid-October, Jehl estimates that from 625,000 to 875,000 Eared Grebes (perhaps 30% of the continental population) are on Mono Lake, California, exploiting the temporary abundance of brine shrimp (*Artemia monica*) and brine flies (*Ephydra hians*) available to those few avian species that can tolerate the highly saline water. Upon arrival, Eared Grebes become flightless while concurrently laying on vast fat stores, often doubling their arrival weights. During this period, brine shrimp comprise 98% of their diet, and Jehl estimates that at peak numbers grebes on Mono Lake may consume daily 60 to 100 tons of shrimp. By confronting the reader repeatedly with figures such as these, Jehl strikes home the importance of this period in the overall life cycle of the species. He then examines the feeding behavior and molting biology of Wilson's Phalaropes on Mono Lake, drawing parallels between these two halophilic species.

The switch from grebes to phalaropes is rather abrupt, and some readers may question whether the comparisons between two species so different in their taxonomy and biology really work. Each species has its own separate methods and results sections, and my first impression was that this monograph was essentially two manuscripts spliced together under one package for convenience, rather like the modern dissertation written in paper form. The introduction and discussion tie the two studies together well, however, and I found that Wilson's Phalaropes provided a nice comparative contrast to the grebes, even though their overall numbers are much less impressive. As emphasized in the title of the book, what links these two species together is their heavy reliance on inland saline lakes for meeting their fall energy needs.

I recommend this monograph to anyone interested in the migration and post-breeding biology of birds. It provides a nice case history of one of the most striking molt migrations found in North America.—Gary L. Nuechterlein.

SHORT REVIEWS

Birds of Colonial Williamsburg: A Historical Portfolio. By Alan Feduccia with paintings by H. Douglas Pratt. The Colonial Williamsburg Foundation, Williamsburg, Virginia. 1989:162 pp., 75 colored paintings. $29.95.—A "coffee table" book illustrating 75 species of birds which are more or less common in the Williamsburg area. The short accounts of each species by Alan Feduccia generally are informative, and in most cases include remarks by Mark Catesby, John Lawson or other early naturalists about the birds. The centerpiece of the book is the collection of full-page portraits by Doug Pratt. These are usually successful in depicting the species, but in a few of them the birds are much too plump. In many cases the backgrounds suggest the ambience of the Williamsburg scene. Pratt is not afraid to draw the birds in unconventional poses and is usually successful in this, although in some cases he loses the Gestalt of the bird.

The paintings of the Bald Eagle, (*Haliaeetus leucocephalus*), Passenger Pigeon (*Ectopistes migratorius*), and Carolina Parakeet (*Conuropsis carolinensis*) are excellent reproductions of the paintings by Catesby. The reproduction of all the paintings is excellent.—George A. Hall.

Field Guide to the Birds of Britain and Europe. By Jim Flegg. Cornell University Press, Ithaca, New York. 1990:256 pp., many color plates, and maps. $43.50 (cloth), $19.95 (paper).—Another field guide to British Birds! How many are there? The strong point of this guide is the set of photographs. While there is argument as to the suitability of photos

as illustrations in an identification manual, this book is well worth having for the collection of color photographs alone. Most of these were taken by Eric and David Hosking, and to my eye are one of the finest collections of portraits of European birds available. As a field guide it follows standard form: a paragraph on identification, some hieroglyphics indicating habitat, and a small range map, which for once has a good contrast between the colors representing seasonal distribution.

There is a brief introductory discussion of bird biology, a section describing the habitats, and a closing section entitle "Practical Birdwatching."

Readers of the *Bulletin* who do not own a European guide might consider this one, and all American bird students might desire this excellent set of photographs.—George A. Hall.

Men and Birds in South America 1492–1900. By R. Stowell Rounds. Q.E.D. Press, 155 Cypress Street, Fort Bragg, California. 95437. 1990:190 pp., 11 black-and-white photos and drawings, 3 maps. Paperback. No price Given.—While arranging specimens of Dendrocolaptids at the Carnegie Museum, I was puzzled by the number of specimens collected by "Mrs. H. H. Smith." Who was she? Among the many other things in this little book, I learned about her and her husband. Mr. Rounds has compiled for us a brief history of ornithological exploration in South America prior to 1900, including short biographical sketches of practically everyone who worked in South America during the time period selected. These range from people even more obscure than Mrs. Smith to such well known scientists as Darwin, Alexander Agassiz, and Frank Chapman. Of particular interest are the sketches of many people know to most of us only as the describers of bird species, i.e., DeLattre, von Berlepsch, or Natterer. Unfortunately there are some errors of fact in the text, and the number of misspellings and typos indicate that editing or proof-reading has been minimal.—George A. Hall.

Survey Designs and Statistical Methods for Estimation of Avian Population Trends. Edited by John R. Sauer and Sam Droege. U.S. Fish and Wildlife Service Biological Report 90(1), 1990:166 pp. (Available gratis from Publications Unit, U.S.F.&W.S., Room 130 Arlington Square Building, 18th and C Streets N.W., Washington, D.C. 20240).—This is a collection of 26 papers given at a workshop held by the Branch of Migratory Bird Research and the Office of Migratory Bird Management in 1988. Ten papers comprise the first part, Surveys used to Estimate Avian Trends. These describe the Common Bird Census in the United Kingdom, the International Shorebird Survey, as well as the more familiar Breeding Bird Survey and Christmas Bird counts. Part II consists of thirteen papers discussing Methods of Trend Analysis. Part III illustrates the application of the methods in three papers giving an analysis of trends in the Scissor-tailed Flycatcher. The section on Methods should be read by all those interested in interpreting population data.—George A. Hall.

Protecting Internationally Important Bird Sites. By David A. Stroud, G. P. Mudge, and M. W. Pienkowski. Nature Conservancy Council, Peterborough PE 1 iUA. 1990:230 pp., many maps. £17.—This is a useful summary of the establishment of the E.E.C. Special Protection Area Network in Great Britain. Besides listing the sites of importance, and the basis for their selection information is given on the conservation needs of 48 "vulnerable" species and 75 other migratory species. Sixteen of the former and about 40 of the latter are North American birds.—G.A.H.

Characterization of Habitat used by Whooping Cranes During Migration. By Michael J. Armbruster. U.S. Fish and Wildlife Service Biological Report 90(4), 1990:16 pp. (Available gratis from Publications Unit, U.S.F.&W.S., Room 130 Arlington Square Building, 18th and C Streets N.W., Washington, D.C. 20240).—G.A.H.

Boletin sao. Sociedad Antioqueña de Ornitologia, Medellin, Colombia. Vol. 1 No. 1, Junio de 1990—This is an interesting new journal written (in Spanish) at about the level of *American Birds.* The Sociedad hopes to promote local interest in birds and their conservation. Interested North Americans can obtain the journal from the Sociedad at Apartado aereo 60010, Medellin, Colombia for $10 (US).—G.A.H.

XXI International Ornithological Congress

The XXI International Ornithological Congress will be held at the Austria Center in Vienna, Austria from August 21–27, 1994. Its President (Dr. C. M. Perrins, Oxford), General Secretary (Prof. J. Dittami, Vienna) and Scientific Program Committee Chair (Prof. J. C. Wingfield) would like to invite suggestions for symposia and discussion groups to be sent to Prof. Wingfield:

Department of Zoology
University of Washington
Seattle, Washington 98195 U.S.A.

or the organisers:

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Interconvention
Austria Center
A-1450 Vienna, Austria Europe

by July 1991. Symposia should be aimed at reviewing topics of general interest while discussion groups can be more specific.

Suggestions must include a statement of the general theme as well as a list of prospective conveners (including oneself) and contributors with their topics and, if possible, addresses.

Lastly, interested participants are asked to contact the organisers to be put on the mailing list.

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The Wilson Bulletin

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See Wilson Bulletin, 103:163–164, 1991 for more detailed "Information for Authors."

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FIG. 1. Peregrine Falcon (*Falco peregrinus*), 1977, oil. Robert Mengel turns the world on its side in this dramatic scene in which a diving Peregrine Falcon screams headlong into the viewer's world. By counterbalancing the painting's skewed horizon with the tilt of the Peregrine's wings, Mengel ingeniously creates a simultaneous sense of motion and balance. By muting the background and details of the escaping teal, he rivets our attention on the attacking falcon whose blurring wingtips extend beyond the confines of the canvas. Mengel preferred to work in watercolor or pen and ink, but as this powerfully conceived and executed painting reveals, the artist could also work with considerable skill in oil.

FIG. 2. Robert M. Mengel (1921–1990) at work in his Lawrence, Kansas, studio circa 1986.

This essay and future exhibitions of his paintings may begin to help others know more about the artistic ability and achievement of this immensely talented but modest man.[5]

"Talent," explained Mengel, "means the ability to draw something that vaguely resembles something in the real world, without seeming to try. You've either got it or you don't."[6] Robert Mengel clearly had it. His earliest datable drawing—an airplane—captures the romance of flight. It is a small pencil sketch of "The Spirit of St. Louis" in the air, drawn when he saw Charles Lindbergh visit Louisville during the aviator's triumphal tour of 1927. Bobby Mengel was six years old. A pencil drawing of a few years later (Fig. 3) captures a different kind of flight in a subject

that would fascinate him for the rest of his life. It shows a diving Peregrine Falcon dramatically captioned "Nevver [sic] a Pause! Down! Down Down!" In the lower right hand corner is the artist's own contemporary assessment of his work: "fair."

Mengel's qualitative grading of many of his earliest drawings reveals his life-long commitment to improvement through self-criticism. He received no formal training in art, but taught himself to draw by studying his subjects and the work of other artists, honing his innate talent through repeated trial and error.

Though grateful for his natural ability in drawing, Mengel considered it something of a liability, for it brought him a level of praise he felt he did not deserve. "In the eyes of my family I was a prodigy," he recalled,

> and at gatherings of our large clan I would be exhibited with my latest bird pictures. Fame was pleasant, but I suffered mightily because it seemed impossible to communicate with an audience of adults whose ignorance of birds was almost as complete as their adulation of Audubon. 'Dear Bobby,' one or another of my great-aunts would say, 'you'll be a second Audubon!' I could never make them understand that this was not my fondest ambition, and my efforts only magnified my churlishness in rejecting the highest compliment they could offer.[7]

Mengel's life-long fondness for natural history subjects began with a childhood infatuation with reptiles, amphibians, and birds.[8] "The way many natural historians of my generation started," explained Mengel, "was as little kids running around with snakes in their pockets and blackbirds rotting in their mother's dresser drawers."[9]

Born in Glenview, Kentucky, now a suburb of Louisville, on August 19, 1921, Robert Mengel was reared by his mother, who encouraged her son's wide-ranging interests and energetic zeal. After her death in 1934, he was taken in by an equally talented and encouraging maiden aunt. Fortunately, at just this time he also found an ornithological mentor and substitute father (his own having been institutionalized in the 1920s). Burt Leavelle Monroe, Sr. (1901–1968), a knowledgeable birder who would eventually serve as president of the Kentucky Ornithological Society, treasurer and president of the Wilson Ornithological Society and treasurer of the American Ornithologists' Union, took Mengel under his wing and devoted many hundreds of hours to his informal education.[10] "I was too naive by far to think of it then," wrote Mengel, "but in memory it is astonishing how much information, common sense, encouragement, and character he imparted or demonstrated without a trace of 'adult' superiority."[11]

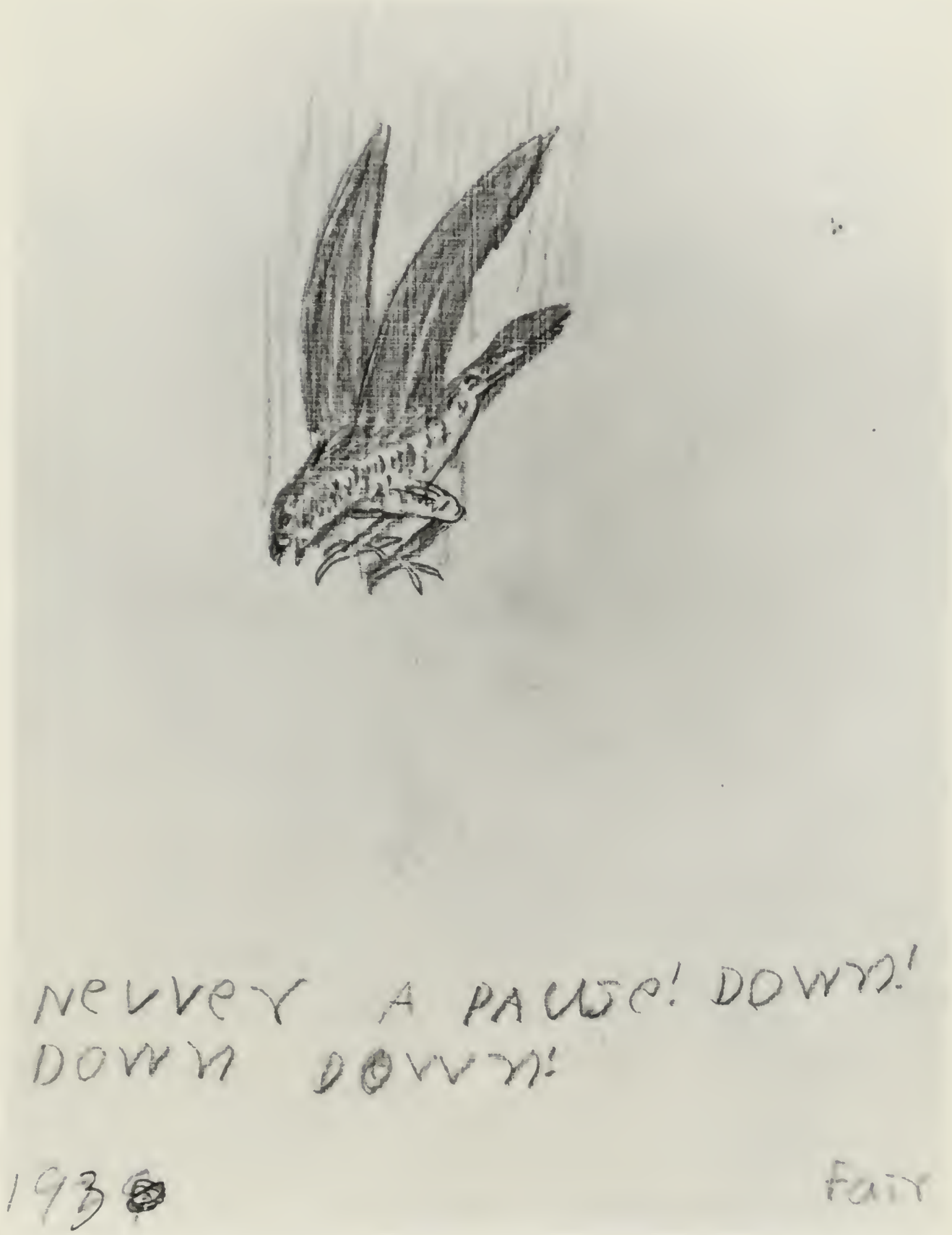

FIG. 3. Bird of Prey in Flight, Kentucky, circa 1930, graphite. From early childhood, Mengel was intrigued by raptors and sought to capture their speed, power and grace on paper. He drew, captioned, and critically graded this example when he was less than ten years old.

FIG. 4. Yellow-crowned Night Heron (*Nycticorax violaceus*) Kentucky, 1941, watercolor. In 1940, Mengel matriculated at Cornell University where George Miksch Sutton (1898–1982) encouraged him to develop his talent for bird painting. Mengel's life studies—this one painted during a return trip to his home-state of Kentucky—soon reached a level of excellence surpassed only by Sutton and his mentor, Louis Agassiz Fuertes (1874–1927).

As a teenager, Mengel spent many "mirthful" after-school hours at Monroe's house "examining specimens and talking ornithology and many other things."[12] Whenever possible, he joined Monroe and his son, Burt, Jr., for weekend outings near and far:

> Most of these trips were necessarily carried out near Louisville. We were often out until after dark, returning tired out and laden with birds to be skinned, nests, eggs to be blown (still respectable in those days), and other objects. There were no limits to Burt's enthusiasm for either birds or foolishness. . . . On rare occasions we drove to the wilder parts of Kentucky, either in the mountainous east or the lowland west, staying overnight in the simple 'tourist courts' of the day and leaving them liberally sprinkled with corn meal and feathers.[13]

These excursions helped Mengel to build his field skills and led to some memorable adventures. "Once," he recalled, "we almost blundered into a moonshine still in full operation. Such was Burt's rustic charm with the impressively armed operators that we ended with the risk to our sobriety being far greater than that to our skins."[14]

In 1937, the year he left Louisville for boarding school in Pennsylvania, Mengel joined the Wilson Ornithological Society.[15] He became a member of the A.O.U. in the following year.

In his free time between academic and athletic commitments at The Hill School, Mengel pursued his interest in both birds and art. Like most aspiring bird painters of the period, he was heavily influenced by Louis Agassiz Fuertes (1874–1927), whose paintings dominated the ornithological literature of the day and whose thorough knowledge of his subject filled Mengel with admiration then and throughout his life. "Fuertes probably possessed the most thorough understanding of birds of any artist of any kind," he wrote.[16]

Fuertes's long association with Cornell and the university's well-established reputation as a center for ornithological study, made it a natural choice for Mengel when he was considering college. On a scouting trip to Ithaca in May 1940, Mengel had a chance to visit the very room in which much of Fuertes's work was created. His host and guide for this pilgrimage was none other than George Miksch Sutton (1898–1982), Fuertes' most distinguished student, and a major artistic figure in his own right. Sutton was then teaching ornithology at Cornell and living in what had been Fuertes' studio.

The two men hit it off immediately and established a life-long friendship. Mengel was entranced by Sutton's paintings and captivating personality. "I had never seen anything on paper like those crisp, lively, bright-eyed birds," he later recalled, "and I had certainly never met anyone at all like this man."[17]

So strong was the Fuertes/Sutton influence on Mengel during his undergraduate years at Cornell that his paintings of the period grew uncannily similar to theirs. Were they not signed and dated, some of Mengel's

watercolor head studies from 1940 and 1941 might easily be attributed to his mentor. The most stylized of these, a series of duck heads, were painted from stuffed birds in sunlight under Sutton's direction.[18] Some of the others—a Yellow-crowned Night Heron (Fig. 4), a Fuertes Red-tailed Hawk, a Red-breasted Merganser, and a Cooper's Hawk—all painted from fresh specimens or observations of live birds, evoke the power of Fuertes or Sutton at their best.

Almost a decade after their first meeting, Sutton asked Mengel to provide some paintings for an article he was writing for *Audubon Magazine* about the use of baby birds as artistic models.[19] Since this was the subject for which Sutton himself was deservedly famous, the invitation was a tremendous compliment to the younger artist. Mengel's professional collaboration with George Sutton would almost certainly have come sooner had World War II not intervened (see Fig. 9).

Robert Mengel joined the U.S. Army Air Force in 1942 and, after a brief period of training, applied to Officers Candidate School with the following letter of recommendation in hand:

> To Whom It May Concern:
>
> I have known Robert M. Mengel for several years. He did a good deal of work with me at Cornell University and this gave me an opportunity to observe him closely. He is a born ornithologist and bird artist. This is saying a good deal, for a good many ornithologists are not born so. He is deeply interested in ornithology, works hard at it, and has attained some eminence in the field especially in so far as Kentucky bird-life is concerned.
>
> Bob's interest in birds does not hide certain other important attributes, among them an excellent memory; enjoyment of working with, and being with, his fellows; ability to concentrate; and an innate tendency to plan with care a course of action. These are attributes a good leader should have.
>
> Sincerely yours,
>
> G. M. Sutton
> Captain, Air Corps[20]

Not knowing quite what to make of such qualifications, the Army assigned Mengel to Airways Communications and sent him to the Middle East. He spent 21 months in Libya, Egypt, and what is now the United Arab Emirates. His drawings of fellow soldiers and military installations there reveal his growing versatility as an artist. A 1945 sketch of two men overlooking the Persian Gulf evokes the loneliness and boredom of Army

FIG. 5. Servicemen on the Beach, Jask, Iran, 1945, graphite. During World War II, Mengel's military service included a tour of duty in the Middle East where he continued to expand his artistic and ornithological skills. In this sketch Mengel captures the boredom and loneliness he and others experienced during periods of the war. In addition to scenes of military life, his wartime sketchbooks are filled with drawings of birds.

life with a masterful economy of line. Many of his other wartime drawings capture the youth and innocence of his friends during this difficult time.

Birds were frustratingly scarce in the desert regions to which he had been assigned. Nevertheless, Mengel managed to find enough birds—and enough free time—to pursue some ornithological interests even under the restrictive exigencies of war. He organized some of his watercolors from the Middle East as an informal field guide to the birds he had seen there.

Mengel's less conventional works during this period include two large watercolors which he intended to submit as possible cover designs for *Audubon Magazine*.[21] The paintings of flamingos and shorebirds are unlike any of his other work. Their highly stylized treatment, bold composition, and limited palette have a strong art-deco flavor, without losing their integrity as accurate depictions of the natural world. This brief experiment with the popular style of the era was the closest Mengel ever came to the field of commercial art.

At the close of World War II, Mengel returned to Cornell to complete his undergraduate degree.[22] He then moved to Ann Arbor to pursue his

FIG. 6. Saw-whet Owl (*Aegolius acadicus*), Michigan, 1949, watercolor. Following World War II, Mengel returned to Cornell and later moved to Ann Arbor to pursue graduate studies at the University of Michigan. His studies from this period are among his best, capturing the essential features of his subjects without overworking the details. "Watercolor is an unforgiving medium," he observed. "It's like ski-jumping—you can't turn back."

master's and doctoral degrees in zoology at the University of Michigan.[23] His paintings during this period show a return to the powerful portrait style of the early 1940s in which he focused on capturing the spirit of his subjects as well as the physical aspects of their anatomy, posture, and

plumage. In a series of owl and raptor studies of the late 1940s and early 1950s, Mengel again approaches the quality of Fuertes and Sutton at the heights of their respective careers.

Equally impressive are his portraits of upland game birds (he was an enthusiastic sportsman) and warblers—to name just two groups of birds that especially interested him at the time. In these, Mengel's first-hand field knowledge and total familiarity with his subjects is self-evident. His deft and confident brushwork, his skilled handling of color, light and shadow, and his intuitive grasp of form are often infused with a sympathy for the subjects that carries them well beyond literal depictions. Although few of these individual studies were ever turned into formal paintings, many stand as minor masterpieces of their kind.

In 1953, while still working on the text and illustrations for his massive "Birds of Kentucky," Mengel took a half-time position at the University of Kansas, cataloging the library's recently-acquired collection of rare ornithological books (the Ralph N. Ellis collection).[24] There his daily access to the beautifully illustrated volumes in the collection enabled him to develop an extensive knowledge of the history of ornithology and scientific illustration.

During his early years in Lawrence, Mengel leavened his ornithological research with a study of dog–coyote hybridization, much of which he based on observations of the offspring of his own terrier bitch and a pure-bred coyote that lived for a while in his house.[25] Naturally, the animals attracted his artistic eye as well, resulting in a series of charming watercolor studies. The accuracy and individuality of each pose—often captured with the barest minimum of brushwork—speak volumes about Mengel's ability to observe and spontaneously record the personalities of his subjects.

In 1962, after 11 years of work, Mengel completed the "Birds of Kentucky" and plunged into another gigantic project, the illustrations for the American Ornithologists' Union's multi-volume "Handbook of North American Birds."[26] In the hundreds of individual black and white portraits he drew for the "Handbook" over the next two and a half decades, Mengel combined traditional India ink renditions with more experimental scratchboard techniques. Working closely with the "Handbook"'s editor, Ralph Palmer, Mengel developed a distinctive illustration style which integrated avian appearance and behavior with depictions of characteristic habitat. His effective use of solid and void, and the effortless balance of his compositions make each of the book's illustrations a visual delight as well as an instructive complement to the text.[27]

George Sutton spoke for many readers when he admired the results. "In my opinion your work is both good illustration and good art," he wrote Mengel in 1962.

FIG. 7. Spotted Sandpiper (*Actitis macularia*) juvenile, New York, 1947, watercolor. Mengel's knowledge of bird anatomy and his deft handling of watercolor enabled him to paint juvenile birds with a fidelity matched by few other artists. In 1949 George Sutton invited him to provide several pictures for an article he was writing on "Baby Birds as Models" for *Audubon Magazine*. Mengel's Spotted Sandpiper was among the group selected by Sutton for publication.

I can't tell you how I enjoy the freedom from cross-hatching and the occasional complete omissions of line where no line is needed. . . . I get a tremendous kick out of this work, not alone because it is exciting as it stands, but also because it bespeaks a remarkable potential and future.[28]

FIG. 8. Lesser Scaup (*Aythya affinis*), Virginia, 1955, watercolor. In this "bird's eye view" of a Lesser Scaup, Mengel creates the varied textures of water, feathers, bill, and eye with subtle changes in brushstroke. His low angle and foreshortened perspective create an illusion of motion, as if the bird has just been startled and is swimming away to safety. Such original concepts of composition give Mengel's watercolors a fresh, lifelike quality rarely achieved in paintings of this kind.

The future for Mengel was a move away from bird painting per se. Although he continued to love birds—and to paint them brilliantly—he painted them as part of a broader experience. In his non-commissioned painting, he focused more and more on landscape, incorporating wildlife

FIG. 9. Greater Prairie Chickens (*Tympanuchus cupido*), Kansas, 1958, pen and ink. When Mengel sent this pen and ink drawing to George Sutton in 1958, Sutton responded enthusiastically: "By golly your Prairie Chickens are nice! The sweep of habitat below the flying birds is really magnificent and your drawing of the upcountry prairies is something to comment about! Only he who draws birds knows what know-how this sort of thing represents. I congratulate you, my good friend."

as enlivening elements to an overall composition, rather than the subjects of central importance. Quite apart from any birds he might choose to include, he wanted each of his paintings to stand on its own as a work of art.[29]

"I have just submitted three pictures to the annual Kansas Watercolor Society show," he wrote George Sutton in 1978.

> I have enjoyed some modest success recently with smaller juried shows and, of course, have been smart enough to leave the animals out or, at the most, much sublimated in the landscape. I have become persuaded that Carl Rungius was right, namely, make a name in the field of general art (if you can) and *then* emerge as a closet bird (mammal) painter, easy of mind and thumbing your nose at the provincial of both persuasions![30]

In "Beauty and the Beast," Mengel quoted George Sarton, the historian of science, as saying: "works of art are precious to us, above all, because they enable us to understand . . . as we could in no other manner, the people who produced them. Each gives us an intuitive, synthetic, and immediate knowledge of their deepest aspirations."[31] In his own copy of the article, Mengel underlined the quote and noted "I have found it useful to return often to these words."[32]

It is not by chance that in Mengel's paintings we see bits of Carl Rungius,

FIG. 10. Scissor-tailed Flycatcher (*Tyrannus forficatus*), 1987, pen and ink, published in "Guide to Bird-finding in Kansas and Western Missouri" by J. L. Zimmerman and S. T. Patti (1988). As an artist, Mengel is probably best known for the many black and white illustrations he created for publication. A brilliant draftsman with an instinctive eye for composition, Mengel distilled the essence of his subjects and placed them in stylized but entirely characteristic habitats. The resulting images are often as evocative of time and place as they are of the birds depicted. (Courtesy, S. T. Patti).

Ogden Pleisner, Andrew Wyeth, Eric Ennion, Bruno Lilejefors, Winslow Homer, George Miksch Sutton, Robert Verity Clem, Frances Lee Jaques, Louis Agassiz Fuertes, and a dozen or more other artists whose work he admired, for with these artists he shared common approaches to art.

Despite such affinities, except in his early paintings, very little of what he created with pencil, pen and brush was derivative. Where stylistic overlap with others did occur, it reflects not emulation so much as a convergence of objectives and achievement.

The pictures he made throughout his life were filled with joy and light, and love of the outdoors. He reveled in the freedom of wildness on every scale: Golden Plovers in an Alaskan meadow, Prairie Chickens booming

FIG. 11. "Carman in the Snow," Coyote (*Canis latrans*), Lawrence, Kansas, 1955, watercolor. Mengel's scientific interest in coyotes and coyote–dog hybridization took on a highly personal dimension when he decided to have the animals live with him at home. They soon became a part of his extended family, and the subjects of his pen and brush. As this watercolor study reveals, the artist's ability to convey the external appearance, behavior, and even the personality of his animal subjects was by no means limited to birds. (Courtesy, S. T. Patti).

to a Kansas dawn, a mink sunning by one of the Montana spring creeks he loved to fish, or a pair of Golden Eagles dancing in a clouded western sky.

My favorite is a loose wash of streamside vegetation with a bleached drift log reflecting in a quiet pool (Frontispiece). Two thirds of the way up the paper and slightly to the left of center is a soaring sharpshin. The hawk, fluid, almost casual, yet precisely composed and rendered, infuses the painting with spontaneity and life. In "Sharpshin," as in a number of his later works, Mengel managed to transcend the accurate replication of nature. At the height of his artistic power, he was able to recreate the intangible sensations of experience.

In the written, drawn and painted work that punctuated his career, Robert Mengel went a long way to bridging the "gulf of mutual incomprehension" between science and the humanities described by the British author C. P. Snow.[33] His rare combination of artistic talent, technical competence, intellectual acumen, and emotional involvement with his subjects, enabled him to effectively blur the boundaries of science and art. In so doing, he created a legacy that is at once comprehensible, instructive, and inspiring to the proponents of both.

ACKNOWLEDGMENTS

This appreciation of Robert Mengel and his art, originally suggested by Ken Parkes, is based on a reading of Mengel's many published and unpublished writings, a comprehensive

review of his art, and my own long admiration of his artistic, literary, and scientific contributions to the field of ornithology. For a more personal perspective on Robert's life, and for her invaluable help in making his art work accessible to me, I am deeply grateful to Marion Jenkinson Mengel.

I am also indebted to the friends and colleagues of Robert Mengel to whom I turned for personal insights and advice. For their many thoughtful suggestions and enthusiastic encouragement, I would especially like to thank R. Clem, C. Dwigans, D. Eckelberry, F. Gill, M. Hill, F. Lohrer, J. O'Neill, R. Palmer, K. Parkes, V. Pine, G. Schnell, G. Tudor, H. Tordoff, and G. Woolfenden.

ENDNOTES

[1] Robert Mengel, "Beauty and the Beast," *The Living Bird,* Cornell Laboratory of Ornithology, Ithaca, N.Y., Vol. 18, July 1980, p. 41.

[2] Robert Mengel, "Bibliography and the Ornithologist," in Thomas R. Buckman, ed. "Bibliography & Natural History," Lawrence: Univ. of Kansas Libraries, 1966 p. 121.

[3] "A Catalog of the Ellis Collection of Ornithological Books in the University of Kansas Libraries" compiled by Robert M. Mengel, Vol. 1, A–B, 1972; Vol. 2, C–D, 1983. Vol. 3, E–G, is still being prepared for publication.

[4] "The Birds of Kentucky," A.O.U. Monograph #3, 1965; "The Handbook of North American Birds," Ralph S. Palmer, ed., A.O.U.; "Guide to Bird-finding in Kansas and Western Missouri" by J. L. Zimmerman and S. T. Patti, Univ. of Kansas Press, 1988.

[5] The most recent exhibition of Robert Mengel's painting, for which the author served as guest curator, was displayed in the Oklahoma Museum of Natural History at the University of Oklahoma in conjunction with the joint meeting of the Wilson and Cooper Ornithological Societies, May 1991.

[6] Interview with Robert Mengel by Cathy M. Dwigans and John E. Simmons, 9/25/86, quoted in *Panorama,* Univ. of Kansas Museum of Natural History, Vol. 15, No. 3, Winter, 1986, p. 1.

[7] From a book review of "The Original Watercolor Paintings by John James Audubon," *Scientific American,* Vol. 216, No. 5, May 1967, pp. 155–158. Mengel goes on to discuss the reasons for Audubon's almost universal popularity despite his shortcomings as an accurate illustrator of nature.

[8] When asked by a reporter how he developed an interest in birds, Mengel admitted "I haven't the slightest idea," but then went on to speculate that it had something to do with their "combination of aesthetics and complexity." *Lawrence Journal-World,* January 1, 1984, p. 6A.

[9] Interview with Robert Mengel by Cathy M. Dwigans and John E. Simmons, 9/25/86, quoted in *Panorama,* Univ. of Kansas Museum of Natural History, Vol. 15, No. 3, Winter, 1986.

[10] Robert Mengel met Burt Leavelle Monroe, Sr., through the Beckham Bird Club of Louisville. Monroe served as president of the Wilson Ornithological Society from 1954 to 1956.

[11] Robert Mengel, "In Memoriam: Burt Leavelle Monroe, Sr.," *The Auk,* Vol. 88, No. 1, January 22, 1971, p. 91.

[12] Ibid., p. 91.

[13] Ibid., pp. 91–92.

[14] Ibid., p. 92.

[15] Robert Mengel attended the Hill School in Pottstown, Pennsylvania, graduating with the class of 1940.

[16] Mengel, "Beauty and the Beast," pp. 56–57.

[17] Robert Mengel, "George Miksch Sutton: A Bird Artist's Bird Artist," *The Living Bird Quarterly,* Spring, 1983, p. 30.

[18] This, according to a much later annotation by Mengel on one of the studies.

[19] In a letter to Mengel of June 24, 1948, Sutton writes: "Dear Bob: Recently I've been doing a baby bird a day or better and the collection of baby bird drawings is growing rapidly. I've thought of doing an article for *Audubon Magazine* on baby birds as models, and wonder if you and Bill Lunk would like to let me use one or two of *your* drawings of baby birds as additional illustrations. . . . I liked your Robin study *very much.* . . ." Letter from the estate of Rober Mengel.

Sutton's article, complete with two of Mengel's paintings, appeared under the title: "Baby Birds as Models," see: *Audubon Magazine,* March–April 1949, pp. 104–108.

[20] Letter of recommendation, February 18, 1943 from the estate of Robert Mengel.

[21] In a letter to George M. Sutton from Tripoli, Libya, of June 16, 1945, Mengel wrote: "I have done quite a bit of painting myself from time to time since I have been overseas. Not really a great deal, but at least a few 'field sketches'. . . . In addition to the above-mentioned portraits, I have done two other pictures of a freer type—made with the idea in mind of suitability for covers of magazines—to wit: *Audubon Magazine.* One is of a pair of stone curlews in black and white, the other of three flamingos in

black and white and pink. (I saw quite a number of flamingos in Arabia before I left there). Do you seriously [think] *Audubon Magazine* would consider publishing foreign birds on its cover? That is, assuming the pictures are suitable for reproduction, and of satisfactory quality (which, of course, remains for them to decide)." (A copy of this letter is in the estate of Robert Mengel.) No evidence survives to reveal whether or not he ever submitted the paintings to *Audubon.* They were never published.

[22] Mengel received his B.S. from Cornell in 1947.

[23] Robert Mengel received his Master's degree from the Univ. of Michigan in 1950 and a Ph.D. from the same university in 1958 under the direction of Josselyn Van Tyne and (after Van Tyne's death in 1957) William H. Burt.

[24] In 1967 he was made Curator of Ornithology and Associate Professor of Systematics and Ecology at the Univ. of Kansas. He was given a full professorship in 1971. As his long-time friend Bud Tordoff has written, Mengel found at the Univ. of Kansas "exactly the sort of job he had aimed for, museum curation with some teaching involvement." See: Harrison B. Tordoff, "In Memoriam: Robert M. Mengel," *The Auk,* Vol. 108, No. 1, 1991, pp. 161–165.

[25] According to several of Mengel's friends, his pack of semidomesticated coyotes occasionally escaped. On more than one occsion his study subjects were captured and returned by the police. Thus his study of dog-coyote hybrids (*Journal of Mammalogy,* Vol. 52, 1971, pp. 316–336) may be unique among scientific journals in giving thanks to the local chief of police!

[26] "The Handbook of North American Birds," Ralph Palmer, ed. New Haven: Yale Univ. Press, 1962–1988: Vol. 1, 1962; Vols. 2 + 3, 1976; Vols. 4 + 5, 1988. In addition to the many black and white illustrations Mengel made for this series, he also created 11 full page color plates.

[27] According to Ralph Palmer, the "Handbook"s editor and artist "were of one mind that, where feasible, a humdrum delineation of diagnostic details was out—the illustrations were to be both biologically truthful and esthetic. Typically, the editor supplied a layout (sketch) to which was clipped and written suggestions and often photos. Bob then executed the picutre and sent a facsimile copy to Palmer, a few needed minor changes, which were marked on the copy and this was returned to Bob. Then he corrected the original and it was forwarded directly from the artist to the publisher." Personal correspondence, March 19, 1991.

[28] Letter from George Sutton to Robert Mengel, October 17, 1962, from the estate of Robert Mengel.

[29] "When I paint birds . . . for my own pleasure," Mengel explained, "I don't paint ornithological pictures at all. I try to paint birds as part of an experience, as part of a landscape. The painting ought to be able to stand without a bird, but when the bird comes along, all the better." From an interview with Robert Mengel by Cathy M. Dwigans and John E. Simmons, 9/25/86, quoted in *Panorama,* Univ. of Kansas Museum of Natural History, Vol. 15, No. 3, Winter, 1986, pp. 1–2.

[30] Letter from Robert Mengel to George M. Sutton, from the estate of Robert Mengel.

[31] George Sarton, "Introduction to the History of Science," Vol. 1, Baltimore: Williams and Wilkins, 1927, p. 4, quoted in Robert Mengel, "Beauty and the Beast," op. cit. p. 28.

[32] From Robert Mengel's own copy of "Beauty and the Beast," the estate of Robert Mengel.

[33] C. P. Snow, "The Two Cultures and the Scientific Revolution," Cambridge Univ. Press, 1959, p. 4.

Wilson Bull., 103(3), 1991, pp. 357–365

DISTRIBUTION AND BREEDING BIOLOGY OF THE RED-FRONTED MACAW

Dirk V. Lanning[1]

Abstract.—The Red-fronted Macaw (*Ara rubrogenys*), endemic to Bolivia with a restricted range and a small population, was observed regularly between late December 1981 and early March 1982. Individuals were found at elevations between 1300 and 2400 m in the arid intermontane valleys of south central Bolivia in southeastern Cochabamba and western Santa Cruz departments, where they had been reported previously, and in northwestern Chuquisaca and northeastern Potosí departments. Seven nests were located in cavities in cliffs 15 to 50 m tall. Courtship and incubation activities took place during December and January. Nestlings were present during February and March. *Received 10 Dec. 1990, accepted 28 March 1991.*

The Red-fronted Macaw (*Ara rubrogenys*) is a little-known psittacine, previously reported from the departments (dptos.) of Cochabamba and Santa Cruz in central Bolivia (Forshaw 1978). Carriker collected a male in Oct. 1937 from Ele Ele (Fig. 1; Bond and Meyer de Schauensee 1942, 1943). Romero (1974) captured 10 specimens in 1973 and early 1974 for the live-bird trade from an unnamed valley in Dpto. Cochabamba. R. S. Ridgely (1981, pers. comm.) observed flocks of up to 80 macaws during March and April 1977 in several valleys in western Dpto. Santa Cruz and adjacent Dpto. Cochabamba. Beginning in 1979, Wells (1981) obtained the macaws for aviculture from Valle Grande, 50 km southeast of Pulquina (Fig. 1).

Ridgely (1981) was told by local residents that the macaws nested semicolonially on certain cliffs from September to February. He was shown one inactive site, said to be used by one or two pairs. Wells (1981) mentioned that he observed collectors taking an unstated number of nestlings from burrows in cliffs and that some burrows went about 3 m into the cliffs. There are no other references on nesting Red-fronted Macaws.

I traveled in Bolivia from December 1981 to March 1982. I observed Red-fronted Macaws in various parts of their known range, looked for the macaws in similar habitat outside of dptos. Cochabamba and Santa Cruz, searched for their active nests, and talked with residents familiar with the species.

STUDY AREA AND METHODS

I studied macaws in the arid intermontane valleys along the eastern slope of the Andes in south central Bolivia (Montes de Oca 1982). The high plains ("altiplano") and mountains

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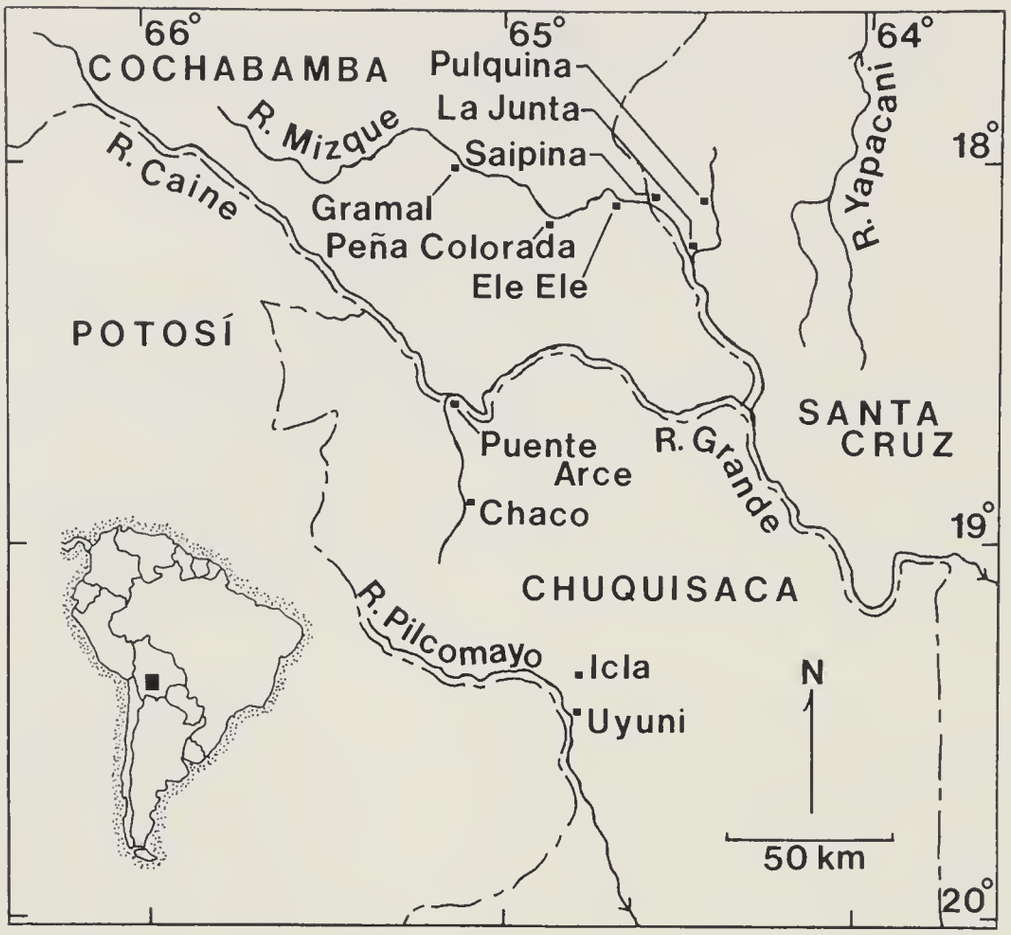

FIG. 1. Map of south central Bolivia showing the departments, localities, and rivers discusssed in the text.

("cordilleras") of the Andes are mostly between 3000 and 6000 m elevation. Dissecting the eastern Andes ("Cordillera Oriental") are the ríos Mizque, Grande, Caine, and Pilcomayo, which flow generally to the southeast and east, and the headwaters of the Río Yapacani which flow north (Fig. 1). The drainages form a series of intermontane valleys ("valles") that are at 1000 to 3000 m. Along the eastern edge of the Andes, at 500 to 2000 m, is the discontinuous front range ("Frente Subandino"), with gaps where the major rivers exit the mountains. East of the Andes are the lowland plains ("Llanuras") of southeastern Bolivia.

The substrate of the valley region consists of sandstones, conglomerates, quartzites, and limestones (Montes de Oca 1982). Cliffs are present both near the rivers and farther up on the slopes. Many of the cliffs are poorly cemented sandstones and conglomerates, with numerous cracks and cavities.

The valley region has a warm, relatively dry climate. The area is protected from the moisture-laden winds from the north and northeast by an eastward extension of the Andes north of the Río Mizque (Bond and Meyer de Schauensee 1942, Muñoz-Reyes 1980). Mean annual rainfall in the valleys is between 300 and 800 mm, with the majority coming between November and April (Montes de Oca 1982).

Carriker (in Bond and Meyer de Schauensee 1942) described the vegetation at Ele Ele (1450 m) in Dpto. Cochabamba as thorny scrub with a tremendous variety of cactus, some over 12 m tall. He described the higher slopes above Ele Ele (2450 m) as including a fair number of trees 9–12 m in height. Ridgely (1981) described the habitat in western Dpto. Santa Cruz as desert-like shrubby vegetation in the valleys and on the lower slopes (1300–1500 m) and a somewhat taller, although still dry, woodland on the upper slopes and ridges (2000–2200 m).

Montes de Oca (1982) classified the vegetation in much of the arid intermontane valley

region as temperate and subtropical thorn woodland ("monte espinoso") and dry forest ("bosque seco"), based on the life zone classification developed by Holdridge (1967) and applied to Bolivia (Tosi et al. 1975). Similar areas in the northern valleys are classified as subtropical lower montane thorn steppe ("estepa espinoso") and dry forest (Tosi et al. 1975, Montes de Oca 1982). Common Anacardiaceae include *Lithraea* spp., *Shinopsis* spp., and *Shinus molle*; common Cactaceae include *Cereus* spp., *Neocardenasia herzogiana, Opuntia* spp., and *Trichocereus* spp. (Muñoz-Reyes 1980, Montes de Oca 1982). Other common shrubs and trees of the valley region include *Acacia* spp. and *Prosopis* spp. (Mimosaceae), *Cassia* spp. and *Caesalpinia* spp. (Caesalpiniaceae), *Celtis* spp. (Ulmaceae), *Gourliaea decorticans* (Fabaceae), *Maytenus* spp. (Celastraceae), *Jacaranda acutifolia* (Bignoniaceae), and *Zizyphus* spp. (Rhamnaceae), among many others (Montes de Oca 1982).

The vegetation at the higher elevations within the valley region and to the west of the valley region is mostly subtropical and temperate montane and subalpine forest, steppe, and desert scrub (Montes de Oca 1982). The vegetation in the mountains north, east, and south of the valley region is mostly subtropical and temperate moist forest and wet forest (Montes de Oca 1982). The vegetation of the lowland plains east of the valley region is classified as temperate thorn woodland and dry forest (Tosi et al. 1975, Montes de Oca 1982), similar to the habitat in the arid intermontane valleys.

The arid intermontane valleys are rich in endemic species. Six species endemic to Bolivia are found only in this "Valle zone" of the central Bolivian Andes (Remsen and Traylor 1989): Red-fronted Macaw, Wedge-tailed Hillstar (*Oreotrochilus adela*), Bolivian Earthcreeper (*Upucerthia harterti*), Bolivian Warbling-Finch (*Poospiza boliviana*), Citron-headed Yellow-Finch (*Sicalis luteocephala*), and Bolivian Blackbird (*Oreopsar bolivianus*). Five other species are found only in the dry valleys from northwestern Bolivia south to northern Argentina (Remsen and Traylor 1989): Red-tailed Comet (*Sappho sparganura*), Rufous-banded Miner (*Geositta rufipennis*), Rock Earthcreeper (*Upucerthia andaecola*), Brown-backed Mockingbird (*Mimus dorsalis*), and Rufous-sided Warbling-Finch (*Poospiza hypochondriaca*).

I studied the Red-fronted Macaw during six weeks between late December 1981 and early March 1982. I hiked about 340 km up and down the valleys and canyons along the eastern slope of the Andes. I observed the macaws while walking and camping, and made a few observations while traveling on trucks. An unknown number of macaws were counted more than once; however, the numbers provide a comparison of the relative abundance and activity of the macaws in each area. After locating the macaws at possible nest cliffs, I observed the macaws for one or more days, usually from an observation point 50 to 200 m in front of and below the cliff. The behaviors of the adult macaws and the calls of nestlings indicated the stages of the breeding cycle. I did not carry technical climbing equipment and was not able to examine any nest cavities.

RESULTS

Distribution.—I observed Red-fronted Macaws in flight along the valleys of the ríos Mizque, Grande, and Pilcomayo in dptos. Cochabamba, Santa Cruz, Chuquisaca, and Potosí (Fig. 1). I observed 245 macaws during 18 to 27 December and 27 February to 8 March (203 observation hours [h]) along 50 km of the Río Mizque and a tributary between Saipina, La Junta, and Pulquina (1300–2100 m, Fig. 1). I observed 176 macaws during 4 to 10 January (70 h) along 40 km of the Río Mizque between Peña Colorada and Ele Ele (1450–2100 m, Fig. 1). I saw six macaws on

29 December (2 h) farther up the Río Mizque near Gramal (1800 m, Fig. 1). To the south, I observed 51 macaws on 30 December and 2 January (8 h) along 40 km of a tributary of the Río Grande between Puente Arce and Chaco (1600–1900 m, Fig. 1). I observed 14 macaws during 15 to 17 January (22 h) along 20 km of the upper Río Pilcomayo and a tributary, between Icla and Uyuni (2100–2400 m, Fig. 1). These totals exclude the repetitious observations of nesting pairs under observation. During 305 h of observation time, I observed a total of 492 Red-fronted Macaws: 58 single macaws, 101 pairs, and 45 flocks of 3–12 macaws. Remsen (pers. comm.) observed two flocks of 7 and 50 Red-fronted Macaws in late June 1984 near Tambo, about 10 km north of Pulquina (Fig. 1).

I did not travel farther down into the valleys and canyons of the Río Pilcomayo in the southern half of Dpto. Chuquisaca south of Uyuni. On 9 February, I did travel through areas of dry woodland vegetation and cliffs along a stretch of the Río Pilcomayo and its tributaries in northern Dpto. Tarija, about 240 km southeast of Uyuni. I did not see any Red-fronted Macaws, but I did see two pairs of Military Macaws (*A. militaris*) flying along cliffs above the river in the canyon just west of where the river flows out of the mountains and into the lowland plains. I spent two more days travelling in the eastern Andes in Dpto. Tarija but saw no more macaws.

Daily activities away from the nests.—The Red-fronted Macaws were visible and active in the morning (05:30–09:29; $\bar{x}$ = 1.8 macaws/h of observation time), around noon (11:30–13:29; $\bar{x}$ = 1.8 macaws/h), and again in the late afternoon and evening (15:30–19:29; $\bar{x}$ = 2.1 macaws/h). During periods of activity, the macaws were flying up and down the drainages and feeding. I observed the macaws feeding 12 times on fruits of *Jatropha hieronymii* (Euphorbiaceae), a common tree in the valleys (species identified by D. Wasshausen, pers. comm.). Two macaws were seen eating corn (*Zea mays*), and one was nibbling on the fruits on the top of a large columnar cactus (*Cereus* sp.). There were lulls in activity in the late morning (09:30–11:29; $\bar{x}$ = 1.2 macaws/h) and afternoon (13:30–15:29; $\bar{x}$ = 0.8 macaws/h), when the macaws were preening and loafing on cliffs or in the vegetation. The two largest flocks (10 and 12 macaws) were observed in the late afternoon and evening and may have been roosting flights.

Nest sites.—I located seven active Red-fronted Macaw nests along the Río Mizque drainage system in southeastern Dpto. Cochabamba and western Dpto. Santa Cruz (Fig. 1). The nest cavities were inside crevices in cliffs composed of sandstones and conglomerates. All cavities were located in sheer or overhung parts of the cliffs. Nest entrances faced northeast (2), east (1), southeast (1), southwest (2), and west (1). The nests

were between 2 and 20 m ($\bar{x}$ = 9 m) below the top of the cliff and between 10 and 48 m ($\bar{x}$ = 18 m) above the base of the cliff. Three nests were in the top third of the cliff face, and the remaining four were in the middle third of the cliff face. The cliffs were 15 to 50 m tall ($\bar{x}$ = 28 m) and 15 to 600 m long ($\bar{x}$ = 245 m). The bases of the cliffs were 0 to 300 m ($\bar{x}$ = 140 m) above the river and 600 to 1200 m ($\bar{x}$ = 870 m) below the top of the ridge. The elevations of the nests were between 1300 and 1800 m ($\bar{x}$ = 1520 m).

The two closest Red-fronted Macaw nests were 200 m apart on separate cliffs and two other nests were 500 m apart on separate cliffs. There were two active Blue-fronted Parrot (*Amazona aestiva*) nests and six active Mitred Parakeet (*Aratinga mitrata*) nests in cavities on the same cliffs and within 100 m of active Red-fronted Macaw nests. Monk Parakeets (*Myiopsitta monachus luchsi*) build their stick nests on cliffs (Lanning 1991) and had one nest structure 30 m below an active macaw nest. When the various nesting parrots saw other parrots fly to or near the same or nearby cliffs, they often interacted by vocalizing, perching on the cliffs and nearby vegetation, and flying near the cliffs and near each other.

Breeding behavior.—I observed pairs of macaws in the vicinity of their nest cliffs from dawn to dusk during ten complete days (143 h). I made additional observations during parts of eight days (55 h); the behaviors were similar and appeared to confirm the patterns observed during the complete days.

I observed two days of courtship activity (22 December and 5 January) at two cliffs. One pair spent the preceding and following nights in the cavity, and the second pair spent the nights at an unknown location outside the cavity. One pair was together inside the cavity for two periods during the day, and the other pair was in the cavity seven times during the day. Both pairs regularly perched on the cliffs or in the nearby trees, preened each other, and fed each other (by regurgitation). One pair was observed copulating once, just after the male fed the female. One or both macaws at the two cliffs were in the cavity during 37% of the two days, both macaws were in the vicinity (within 100 m) of the cliff during 22% of the days, and both macaws were gone from the area the remaining 41% of the time.

I observed three days of incubation activity (22 and 24 December and 6 January) at three nests. All three pairs spent the nights in the nest cavity. Each pair copulated once during the day's observations, allowing the male and female to be identified by their behavior and then by individual differences in plumage. Two of the females left the nest seven times throughout the day, and the other female left four times. The females at the three nests left the nest for periods of 3–15 min ($\bar{x}$ = 8.0 ± 4.1 [SD])

and were fed by the male, while perched on a limb usually below and in sight of the nest cavity. One or both macaws at the three nests were in the nest cavity during 95% of the three days, and both were within sight of the nest cavity (within 100 m) the remaining 5%. At no time were both macaws gone from the area.

I observed five days of activity during the nestling period (28 February and 1, 3, 6, and 7 March) at three nests. Two adult pairs spent the nights in the nest, and the third pair arrived at the nest cliff 60 min after dawn and left 20 min before dusk. One or both macaws entered each nest 2 to 6 times during the day. Each episode in the nest lasted 14 to 189 min ($\bar{x}$ = 51 ± 49; N = 18). The nestlings had monotone "nyah" calls that were higher and more nasal than the calls of the adults. I heard "gurgling" sounds while the nestlings were being fed; both adults fed the young. At least two nestlings were audible at each of two of the nests. At the third nest the roar of the river drowned out the calls; however, the activities of the adults were similar to the activities at the other nests. One or both macaws were in the nest cavity during 39% of the five days, both were in the vicinity of the nest cliff (but not inside the nest) during 6% of the days, and both were gone from the area the remaining 55% of the time. I did not see the nestlings make their first flight, nor did I see any young birds flying by the time I left the region on 8 March.

DISCUSSION

Distribution.—I found Red-fronted Macaws in western Dpto. Santa Cruz and southeastern Dpto. Cochabamba, where they had been reported by Bond and Meyer de Schauensee (1943), Forshaw (1978), Romero (1974), Ridgely (1981), and Wells (1981). I also found them to the south in northwestern Dpto. Chuquisaca and the northeastern edge of Dpto. Potosí, where they had not previously been recorded (Remsen and Traylor 1989). Forshaw (1989) included the Río Pilcomayo as part of the macaw's range. All individuals were seen along the three major drainages in the intermontane valley region, at elevations between 1300 and 2400 m above sea level. Local residents said that the macaws were present throughout the year along all three drainages.

There are a few recently published references on the macaw's distribution. Nores and Yzurieta (1984) observed 200 Red-fronted Macaws in October 1982 in a corn field 9 km south of Gramal (Fig. 1). Cordier (in Alderton 1985) observed four Red-fronted Macaws near the Río Mizque during April 1970. C. Cordier (in Alderton 1985) has collected Red-fronted Macaws since 1968 for aviculture and has observed an unlisted number near the Río Caine (Fig. 1). Remsen, Traylor, and Parkes (1986) reported a specimen collected in July 1921 at El Palo, about 25 km east

of Pulquina (Fig. 1). N. J. Collar and N. Krabbe (unpubl. data) have several unpublished specimen records from the Río Mizque and Río Grande drainages.

The arid intermontane valleys inhabited by Red-fronted Macaws are nearly surrounded by terrain and vegetation unsuitable to the macaws (Ridgely 1981, this study). Ridgely (1981) suggested that the macaw's range may extend a short distance to the south of the Río Mizque and Río Grande drainages, and, as he predicted, I subsequently found it in the upper end of the Río Pilcomayo valley. The southern limit of the macaw's range along the Río Pilcomayo is not yet known; however, suitable vegetation exists in a narrow corridor along the valley of the Río Pilcomayo for 250 km to the southeast, where the river exits the mountains and enters the lowland plains.

Nest sites.—I found Red-fronted Macaws nesting in cavities in cliffs in western Dpto. Santa Cruz and southeastern Dpto. Cochabamba. Suitable nest sites in cliffs appeared to exist in the canyons and rugged valleys throughout the known range of the macaw. Although several large macaws nest in tree cavities, I did not find any trees in the arid intermontane valleys that could provide nest cavities large enough for the Red-fronted Macaw. The Red-fronted Macaw's cliff nest sites are similar to the cliff nests of some other psittacines, including the Indigo Macaw (*Anodorhynchus leari,* Sick 1981), Military Macaw (Gardner 1972, Ridgely 1981), Scarlet-fronted Parakeet (*Aratinga wagleri*; Meyer de Schauensee and Phelps 1978, Ridgely 1981), and the Maroon-fronted Parrot (*Rhynchopsitta terrisi,* Lawson and Lanning 1981).

Status.—Ridgely (1981) estimated that the total population of Red-fronted Macaws was no more than 1000–3000 birds in an area about 100 km from west to east and 50 km from north to south. The macaw's range is now known to be unevenly dispersed over a 150 km by 180 km area (Fig. 1). Combining Ridgely's estimate of population size and range with current information on the macaw's range and habitat, I estimated that there were 3000 to 5000 Red-fronted Macaws in the wild (Lanning, unpublished report to the International Council for Bird Preservation and New York Zoological Society in 1982). C. Cordier (in Silva 1989) feels that "5000 is a reasonable figure," but suggested that "aggregates were large prior to ravages by bird dealers."

The major threat to the species during the 1970s and 1980s was trapping of up to several hundred macaws annually for exportation to the U.S., Europe, and Japan (Ridgely 1981).

In July 1983 the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) listed the Red-fronted Macaw in Appendix I, effectively limiting and regulating exportation and im-

portation among countries participating in the Convention (Jorgenson and Thomsen 1987). In May 1984, the Bolivian government banned the export of all live wildlife (Jorgenson and Thomsen 1987). However, in October 1984, "surreptitious specimens" could be purchased in Bolivia, and were reportedly being exported abroad in very small numbers from an "adjacent" country (Silva 1989). No Red-fronted Macaws have legally entered the United States since 1983 (Jorgenson and Thomsen 1987, Silva 1989). Silva (1989) believed that the CITES listing should offer some protection from the "ravages of unscrupulous dealers," and the Bolivian government export ban on wildlife was officially extended to at least June 1989 (Gaski 1987).

Now that the species is officially protected from exportation for the live-bird trade, other threats to the continued health of the species may have increased in importance and need to be considered during future studies. Current threats may include direct persecution by residents and by farmers protecting their corn and peanut crops (Romero 1974, Wells 1981, Alderton 1985), the continuing illegal capture and trade of live macaws (Silva 1989), and habitat destruction (Cordier, in Alderton 1985).

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DISTRIBUTION AND NEST SITES OF THE MONK PARAKEET IN BOLIVIA

Dirk V. Lanning[1]

Abstract.—A little-known, distinctive subspecies of Monk Parakeet, *Myiopsitta monachus luchsi,* was observed during 13 days from December 1981 to March 1982 in the arid intermontane valleys in south central Bolivia. Twenty-seven flocks (2 to 22 parakeets per flock) were observed at elevations between 1300 and 3000 m. Seventeen active stick nests were located on cliffs. No nests were found in trees, where the other subspecies always build their nests. A museum search and literature review produced 35 specimens of this subspecies, 32 with specific localities. The known range includes the departments of Chuquisaca, Cochabamba, La Paz, and Santa Cruz. *Received 10 Dec. 1990, accepted 3 April 1991.*

The Monk Parakeet (*Myiopsitta monachus*) is a familiar and generally common bird throughout much of its large range in southern South America (Ridgely 1981, Forshaw 1989). As summarized by Forshaw (1989), the species is primarily a lowland bird, rarely occurring above 1000 m elevation, and is found in low rainfall areas in open forest, trees along watercourses, savannah woodland, dry *Acacia* scrubland, palm groves, farmlands, and orchards. The parakeet is particularly common in the vicinity of human habitation. The nest, unique among parrots, is a bulky structure built from dry twigs placed in the topmost branches of a tree, which contains one or more nest chambers and is occupied throughout the year by one or more pairs (Forshaw 1989).

One subspecies, however, is not common or widespread. *M. m. luchsi* is little-known, seldom recorded, and apparently rare and very local (Ridgely 1981, Forshaw 1989). *M. m. luchsi* is the most distinctive of the four recognized subspecies, with the forehead and fore crown uniformly pale grey and not brownish, the breast uniformly pale grey without barring, the band across upper abdomen purer yellow and less olive, and the outer webs of the primaries pale blue without green margins (Salvadori 1891, Short 1975, Forshaw 1989; including color plate on p. 509). The following notes, by Carriker (in Bond and Meyer de Schauensee 1943:191), are the only published observations of *M. m. luchsi*: "Several flocks of these birds were seen at Ele-Ele . . . moving up in the valley. They are not particularly shy. They were always seen along the river in heavy vegetation." Carriker collected five males and five females at Ele Ele (1450 m elevation, Fig. 1) during 8–17 October 1937 (Bond and Meyer de Schauensee 1942, 1943). There is abundant xerophytic vegetation at Ele Ele, with thorny

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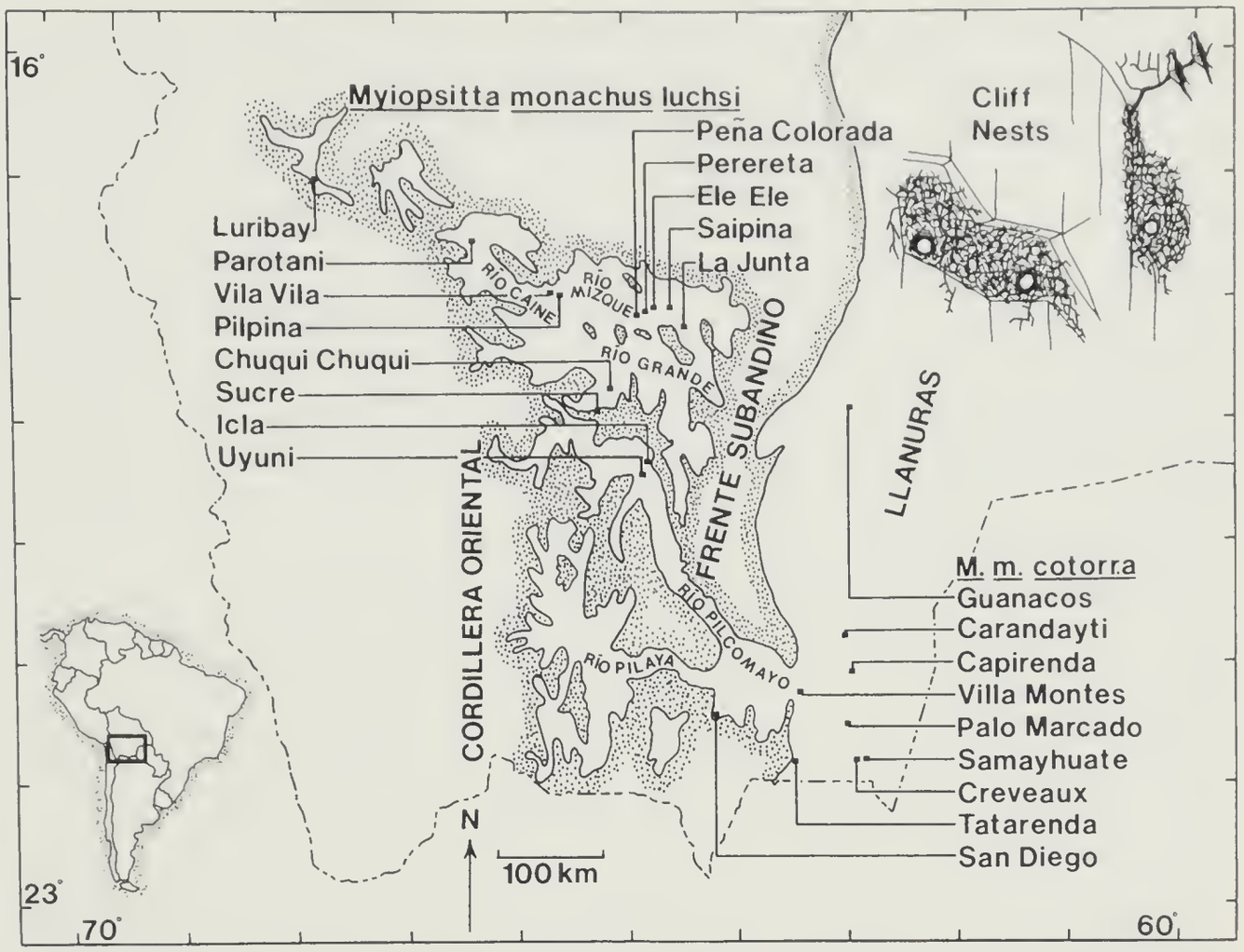

FIG. 1. Map of southern Bolivia with the localities for the Monk Parakeet *Myiopsitta monachus luchsi*) in the arid intermontane valleys and nearby localities for *M. m. cotorra.* The cliff nests are representative of those built by *M. m. luchsi.*

scrub and a tremendous variety of cacti, some 12 m tall (Bond and Meyer de Schauensee 1942).

Ridgely (1981) surveyed the status of parrots in ecologically similar areas east of Ele Ele in March and April 1977 and October 1979 and was unable to find *M. m. luchsi.* I searched for *M. m. luchsi* between late December 1981 and early March 1982 while studying the Red-fronted Macaw (*Ara rubrogenys*) in south central Bolivia.

STUDY AREA AND METHODS

The study was conducted in the arid intermontane valleys along the eastern slope of the Andes in south central Bolivia (Fig. 1). The study area has been described in Lanning (1991).

I searched for *M. m. luchsi* during six weeks between late December 1981 and early March 1982 while hiking 340 km up and down the valleys and canyons of the eastern Andes. I observed the parakeets and their nests on an opportunistic basis, while studying the Red-fronted Macaw (Lanning 1991). All measurements of the parakeet's stick nests and cliffs are visual estimates. I did not carry technical climbing equipment and, therefore, was not able to examine nest chambers. I corresponded with biologists and curators from 1985 to 1989 for information on *M. m. luchsi* and *M. m. cotorra* in southern Bolivia.

RESULTS

Distribution and activities.—I observed 27 flocks of Monk Parakeets (all *M. m. luchsi*) during 13 days between 20 December 1981 and 1 March 1982 in the departments (dptos.) of Cochabamba, Santa Cruz, and Chuquisaca. Eighteen flocks (104 parakeets) were sighted along the drainage of the Río Mizque between Peña Colorado and Ele Ele and between Saipina and La Junta (Fig. 1). Nine flocks (59 parakeets) were sighted in the Río Pilcomayo drainage from near Icla to Uyuni (Fig. 1). The flock size ranged from two to 22 birds ($\bar{x} = 6.4 \pm 4.6$ [SD]). All individuals were in the arid intermontane valleys at elevations between 1300 and 3000 m. The parakeets were locally distributed; I did not find them in many areas of apparently suitable terrain and vegetation.

Monk Parakeets were active throughout the day. When first sighted, 13 flocks were flying, five flocks were in the vicinity of their nests, four flocks were perched on large caraparí columnar cacti (*Neocardenasia herzogiana*), two flocks were perched in *Acacia* sp. shrubs, and three flocks were perched in unidentified trees. The Monk Parakeets ate the small oval fruits on the top of the caraparí cacti and the seed pods of *Acacia furcatispina* (acacia identified by D. Wasshausen, pers. comm.).

Nest sites.—I located 16 Monk Parakeet stick nests on four sheer cliffs (at 1300 to 1800 m) along the Río Mizque drainage and one Monk Parakeet stick nest on a sheer cliff (at 2200 m) along the Río Pilcomayo drainage. Monk Parakeets were active at all cliffs with nests. Parakeets regularly were entering and leaving chambers in the nests, but I was not able to determine the stage of nesting at any of the nests.

The 17 stick nests contained between one and six chamber entrances ($\bar{x} = 2.5 \pm 1.8$). The smallest nest was 0.5 m long and 0.5 m diameter. The largest nest was 5 m tall and 1 m diameter. The volume of the stick nests varied from 0.1 to 5.0 m^3 ($\bar{x} = 0.9 \pm 1.5$). The nests were constructed with interwoven twigs, mostly with thorns. The twigs were usually 20 to 40 cm long. Fifteen nests were anchored to the face of the cliff by twigs wedged in crevices in the rock (Fig. 1). Two nests (1.5 m long and 0.5 m diameter) were hanging over the top edge of a smooth cliff (without crevices), each nest attached with twigs woven around the base of a small shrub growing at the cliff edge (Fig. 1).

The largest cliff, containing three nests, was 50 m tall and 600 m long. There were two nests at a cliff 40 m tall and 100 m long, six nests at a cliff 15 m tall and 75 m long, five nests at a cliff 15 m tall and 40 m long, and one nest at a cliff 10 m tall and 10 m long. All nests were at least 5 m above the base of the cliff, and all but one were on the upper half of the cliffs. The nests were on cliffs that faced west, north, and east. The cliffs were present both near the rivers and on the upper slopes.

Museum specimens.—A museum search and literature review produced

35 specimens of *M. m. luchsi.* (See "Acknowledgments" for museum abbreviations.) The earliest specimen (MNHN; M. d'Orbigny 195), collected in 1829 and examined by Souancé, has "Uruguay, Banda orientale" listed as the locality on the label. Voisin (pers. comm.) feels that Uruguay is probably an error and that "Banda orientale" may mean the oriental part of Bolivia. "Banda oriental" translates as "eastern band or edge" and may refer to the Cordillera Oriental of the Andes. Two adults (BMNH 1846.9.9.41 for both syntypes), collected by T. Bridges and purchased in 1846, have only "Bolivia" listed as their locality (Salvadori 1891).

The other 32 specimens have specific localities. One male (ZMB 87.5) was collected or purchased at Perereta (1500 m, Fig. 1) by F. Behn in April 1847. Two females (ZMB 87.6, 87.7) were collected at Luribay (2600 m, Fig. 1) by A. Stöcker in April 1913; Stöcker's label notes give the impression that these were wild birds (G. Mauersberger, pers. comm.). The Perereta and Luribay locations were mentioned without the additional distribution data in Peters (1937). Two males (BMNH 1902.3.13.1328, 1902.3.13.1329) were collected at Parotani (2500 m, Fig. 1) by P. O. Simons in April 1901. One female and one male (BMNH 1902.3.13.1326, 1902.3.13.1327) were collected at Sucre (2600 m, 2500 m; Fig. 1) by Simons in September 1901. Nine females and four males (SMNH) were collected at Vila Vila (2550 m, Fig. 1) by A. M. Olalla in January 1939. One female and one male (SMNH) were collected at Pilpina (2700 m, Fig. 1) by Olalla in January 1939. Eight of Carriker's 10 specimens from Ele Ele are at ANSP, and two were traded to the U. Mich. Mus. Zool. in 1978 (R. Ridgely, pers. comm.).

DISCUSSION

Distribution.—Bond and Meyer de Schauensee (1943) discuss the specimens from Ele Ele in Dpto. Cochabamba, and Forshaw (1989) states that the subspecies is known only from Dpto. Cochabamba.

There is a recent sighting (19 April 1987, Fjeldså 1987) of an unlisted number of *M. m. luchsi,* in *Prosopis* woodland with large columnar cacti, along a tributary of the Río Grande between Chuqui Chuqui and Sucre (1800 m, 2800 m; Fig. 1). Fjeldså told N. Krabbe (pers. comm., both on the same trip) that there were about five to 10 parakeets flying low.

Based on both observations and specimen records, *M. m. luchsi* has been found at 1300 to 3000 m in the arid intermontane valleys of south central Bolivia. The locations (from north to south) are in the dptos. of southeastern La Paz, southern Cochabamba, western Santa Cruz, and northern Chuquisaca. All records are from the thorn steppe, thorn woodland, and dry forest life zones in the arid intermontane valleys on the eastern side of the Andes.

Nest sites.—*M. m. luchsi* stick nests on cliffs appeared similar to de-

scriptions of stick nests in trees, where the other subspecies always build their nests. Monk Parakeet nests in trees vary in height from nests "easily reached from the ground" in talas (*Celtis tala*) up to nests in the tops of eucalypts (*Eucalyptus* spp.) 30 m tall (Gibson 1919). Monk Parakeet nests in trees are attached among the forking limbs or are hanging from the ends of branches (photos in Laubmann 1930, Naumburg 1930, and Conway 1965; color plate in Forshaw 1989), analogous to the positions of cliff nests attached into crevices or hanging from a small shrub at the top of the cliff. Twigs 40 cm long seemed very large for a bird only 29 cm in length (Forshaw 1989); however, Harrison (1973) found the same species to use twigs about 40–45 cm long at the London Zoo.

I found no evidence that *M. m. luchsi* constructs stick nests in trees. I did not find references to other subspecies of Monk Parakeets building their stick nests on cliffs. I do not know why *M. m. luchsi* nests only on cliffs; there were trees in the vicinity of the cliff nests and throughout the valleys that were of sufficient stature to support the parakeet's stick nests. "Cliff Parakeet" would be an appropriate English name for this bird (Ridgely, pers. comm.).

M. m. cotorra.—Four *M. monachus* specimens (CMNH) were collected at Guanacos (500 m, Fig. 1), Dpto. Santa Cruz, during August 1909 and September 1915 and seven specimens (LACM) were collected 30 km southeast of Carandayti (600 m, Fig. 1), Dpto. Chuquisaca, during July and August 1957 (Remsen et al. 1986). The 11 specimens are all *M. m. cotorra* (K. L. Garrett and K. C. Parkes, pers. comm.). Two *M. m. cotorra* specimens (LACM) were collected at Capirenda (750 m, Fig. 1), Dpto. Santa Cruz, during July 1957. Seven *M. m. cotorra* specimens were collected at Villa Montes (450 m, Fig. 1), Dpto. Tarija, during May 1926 (Laubmann 1930). Laubmann (1930) considered the parakeets infrequent at the edge of the Andes and abundant throughout the lowlands of the Gran Chaco. Eisentraut (1935) observed small flocks of *M. m. cotorra* during the dry season near Villa Montes and found the parakeets and their stick nests abundant farther down the Río Pilcomayo at Palo Marcado and Samayhuate, Dpto. Tarija (400 m, Fig. 1). Lönnberg (1903) wrote of small flocks of about eight or 10 *M. monachus* occurring at Creveaux and Tatarenda (400 m, 650 m; Fig. 1), Dpto. Tarija, from March to May 1902. Two specimens of *M. monachus* were shot at San Diego (1600 m, Fig. 1), Dpto. Tarija, in March 1902 (Lönnberg 1903). These two specimens (SMNH) are indeed *M. m. cotorra* and represent the farthest west and the highest known records for this subspecies.

M. m. luchsi and M. m. cotorra.—There are no specimens intermediate between *M. m. luchsi* and *M. m. cotorra,* despite the fact that their known ranges come within 175 km of each other. Their altitudinal ranges overlap

slightly, and both forms inhabit similar thorn woodland and dry forest life zones. Field work is needed between the known ranges of the two forms along the drainages of the Río Grande and Río Pilcomayo and along the drainage of the Río Pilaya (Fig. 1), a major tributary of the Río Pilcomayo. All of these drainages are accessible by hiking, by river travel via rafts, and by some rough roads. Few, if any, collectors and biologists have ever traversed these rugged valleys and canyons.

What remains unknown is whether Monk Parakeets occur continuously in the region between *M. m. luchsi*'s and *M. m. cotorra*'s ranges in southeastern Bolivia, or whether the apparent gap is real. It is also unknown what types of nest substrates are used in the intervening area. Answers to these questions will determine whether *M. m. luchsi* is worthy of full species status.

ACKNOWLEDGMENTS

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The COOPER ORNITHOLOGICAL SOCIETY will hold its 62nd Annual Meeting at the University of Washington in Seattle, June 22–26, 1992. The meeting will include a variety of events in addition to the scientific program, including a wildlife art exhibition, numerous social events, local excursions to the surrounding Seattle area, outdoor barbecue, pelagic birding, birding trips to Mt. Rainier and North Cascades National Parks, Mount St. Helens National Volcanic Monument, San Juan Islands, and the eastern slope of the Cascades. Dr. David A. Manuwal (Wildlife Science Group, College of Forest Resources, Univ. of Washington, Seattle, WA 98195) will be Local Arrangements Chair. Dr. Dennis Martin (Biology Department, Pacific Lutheran University, Tacoma, WA 98447) will be the Scientific Program Chair.

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TEMPORAL PATTERNS OF SINGING ACTIVITY AT LEKS OF THE WHITE-BELLIED EMERALD

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ABSTRACT.—The White-bellied Emerald (*Amazilia candida*), a sexually monomorphic, dull-plumaged hummingbird, forms singing assemblies that are assumed to function as leks. Within each lek, individuals use and defend specific display perches throughout the day. These perches are visually isolated from one another, and song is the principal form of display. Although some song is given throughout the day, peak activity occurs during the first hour of daylight; a second, more protracted period of display occurs during the 3 hours preceding sunset. The number of songs given by individuals is positively correlated with the number of birds present on the lek, and individuals that are consistently present throughout the day sing more songs when present than do birds that attend the lek only sporadically. *Received 5 Sept. 1990, accepted 19 March 1991.*

RESUMEN.—Amazilia Pechiblanca, un colibrí de plumaje apagado y sin diferenciación sexual, se congrega en formaciones de canto que se asume tienen funciones reproductivas (asambleas reproductivas ó "leks"). Dentro de cada una de estas asambleas reproductivas, los individuos utilizan y defienden perchas específicas a lo largo del día. Estas perchas están aisladas visualmente las unas de las otras, y el canto es la forma principal de exhibición. Aunque cantos aislados ocurren durante el día, la actividad máxima occure durante la primera hora de luz en la mañana; un segundo período de actividad ocurre durante las 3 horas previas a la puesta del sol. El número de cantos que cada individuo exhibe está positivamente correlacionado con el número de aves presentes en cada una de estas asambleas reproductivas, y los individuos que están presentes en estas asambleas reproductivas en forma constante cantan mas que los individuos que están presentes solo en forma esporádica.

Bird species with lek mating systems are often characterized by pronounced sexual dimorphism (Payne 1984). However, Trail (1990) found that approximately one-quarter of all lekking birds were sexually monomorphic in size and plumage, thus raising the question of how monomorphism may persist under the intense pressures of sexual selection that generally characterize lek systems (Bradbury and Gibson 1983, Beehler and Foster 1988). Höglund and Lundberg (1987) and Höglund (1989) proposed that vocal behavior may represent "an alternative target of selection" in monomorphic lek species. In contrast, Trail (1990) suggested that monomorphism in lek birds may result from intense intrasexual competition among both males and females; in this assessment, "social

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selection on females has counterbalanced sexual selection on males to produce monomorphism as an evolved dynamic equilibrium."

Further debate about these hypotheses is hindered by the general lack of data concerning monomorphic, lekking species (Trail 1990). The White-bellied Emerald (*Amazilia candida*) is a small, sexually monomorphic, dull-plumaged hummingbird distributed in Central America from southern Mexico to Nicaragua (American Ornithologists' Union 1983). Although Stiles and Skutch (1989) briefly mentioned that "males may form loose courtship assemblies," no other information appears to be available concerning the behavior of the species. In this study, we present a preliminary description of song behavior in White-bellied Emeralds, including evidence that singing assemblies function as leks. Furthermore, we summarize available data concerning the occurrence of lek behavior in the Trochilidae.

STUDY AREA AND METHODS

We studied White-bellied Emeralds in the Rio Bravo Resource Management and Conservation Area of the Orangewalk District of northwestern Belize (17°50'N, 88°55'W) from 14 February–16 March 1990. On average, these dates coincide with the beginning of the dry season (<100 mm rainfall per month) (Wright et al. 1959). Daily temperatures ranged from approximately 18–27°C; on the night of 18 February, temperatures dropped to approximately 10°C as a result of a major cold front. The moist, subtropical habitat of the Rio Bravo area has been described as "medium-high, semi-deciduous forest" (Pennington and Sarukhan 1968) or "upland broadleaf forest" (N. Brokaw, pers. comm.). Although the area was probably cleared to varying degrees by the Mayan civilization, for the past 900–1000 years the forest has experienced relatively undisturbed regrowth with managed selective logging, and it presently is in a late successional stage. Vertical structure of the habitat is heterogeneous; most upper canopy trees range from 20–30 m in height, with a fairly dense understory of shrubs and saplings. Important families of trees represented in the upland broadleaf forest include Sapotaceae, Leguminosae, Moraceae, Apocynaceae, Meliaceae, and Palmae (N. Brokaw, pers. comm.).

We identified, marked, and mapped the locations of song perches used by White-bellied Emeralds during several days of preliminary observations at each of three leks (A, B, C). Later, on two consecutive days at each lek, we counted the number of songs delivered by six birds at Lek A, three birds at Lek B, and four birds at Lek C; counts recorded the total number of songs delivered by each bird during 48 consecutive, 15-min periods, from 06:00 to 18:00 h. We were unable to capture and uniquely mark individual birds. However, we assumed that we could distinguish individuals based on their highly stereotyped use of specific song perches and our frequent ability to have all singing birds under simultaneous observation by up to seven assistants. In addition to the 312 h of focused observations, supplemental data were collected during numerous, shorter visits to nine additional leks.

Temporal patterns of singing behavior were analyzed using a standardized index of daily song activity, as measured by the percent of an individual's daily total songs that were delivered during each 15-min period. Birds that gave many songs during a day were thus weighted equally with birds that sang few songs. Individual percentages were then used to calculate a mean percentage for each period on a given date. Because low light intensities

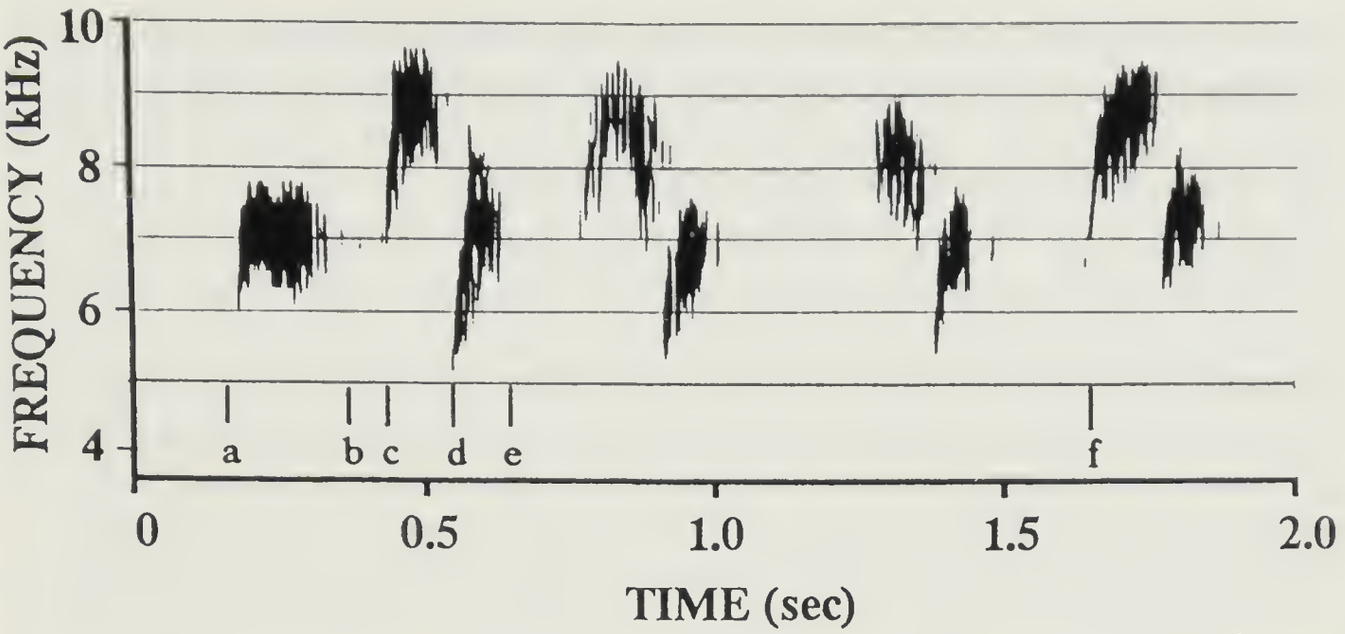

FIG. 1. Song characteristics used in analysis of temporal variation. INTRO = average frequency (kHz) of introductory note, located between a and b; FREQ-I = average frequency (kHz) of first syllable of first paired phrase following the introductory note, c–d; FREQ-II = average frequency (kHz) of second syllable of paired phrase, d–e; LAG = time (sec) between starts of the first and second syllables, d–c; DELIVERY = number of paired phrases delivered per sec, based on time interval from c–f. Additionally, the number of paired phrases delivered in each complete song (PAIRS) was counted.

made it impossible to locate singing birds immediately prior to sunrise, we excluded songs given before 06:00 h.

To evaluate daily variation in vocalizations, we tape recorded songs given from a single perch, presumably by the same individual, at five different times on 10 March. Recording equipment consisted of a Marantz PMD221 cassette recorder, a Sennheiser ME88 directional microphone, and TDK IECII/Type II High Position tapes. We used a Kay Elemetrics DSP Sona-Graph model 5500 to analyze five randomly selected songs representing each time period. Song parameters measured directly from the digital display (Fig. 1) included (1) INTRO—average frequency (kHz) of single, introductory note, (2) FREQ-I—average frequency (kHz) of the first syllable of a song's initial paired notes, (3) FREQ-II—average frequency (kHz) of the second syllable, (4) LAG—time (sec) between start of the first and second syllables, and (5) DELIVERY—number of paired notes given per second. Additionally, we counted the number of paired notes (PAIRS) in all songs recorded during the five time periods.

RESULTS

General description of lek behavior.—A total of 12 White-bellied Emerald leks were observed. Eleven leks were located adjacent to abandoned logging roads where the forest canopy was intact overhead; one lek was found along a 2-m-wide dry stream bed, again with a closed canopy. We found no leks in approximately 10 km of edge habitat located adjacent to a large (15–20 m wide) road where the forest canopy was broken; most display territories within leks were not situated in distinct open areas or edge habitat. The two closest leks were separated by approximately 0.5

km of continuous forest habitat. However, because our exploration of the Rio Bravo area was essentially limited to irregularly spaced roads or trails that provided access into the dense vegetation, we have no data regarding the actual density of White-bellied Emerald leks.

At three intensively studied leks, minimum estimates of the number of birds regularly present were six (Lek A), three (Lek B), and seven (Lek C). Lek members appeared to defend territories of up to approximately 450 m^2 that included two to three specific song perches. The location of these perches appeared to be largely stable throughout the month-long period of our study. Nearest neighbor distances between the approximate center of each territory varied from 14–32 m ($\bar{x} = 25.8 \pm 6.5$ [SD], N = 13). Territories on Leks A and C were spatially distributed such that one or two individuals held what might be considered "central" locations; no central territory was evident in Lek B, which included only three birds dispersed approximately equidistant from each other.

Typical song perches were located on slender, bare branches or lianas that extended into relatively open portions of the mid-canopy. Most were 10–15 m above ground level, although three birds with territories located in lower (3.5–6 m), seasonally inundated riverine vegetation sang from perches only 3 m high. Because of dense vegetation, distance, and in some cases topography, most displaying individuals probably could not see their nearest neighbor. Although each lek member was in audio contact with at least one, and usually more, adjacent territory holders, some birds were separated by as much as 120 m and probably could not hear each other's songs.

Lek displays appeared to consist entirely of song, which generally included a variable number of repeated, paired notes (Fig. 1) that were usually delivered while perched. Detailed characteristics of these songs differed dramatically among leks but were consistent within leks; these data will be presented elsewhere. Singing birds rapidly moved their heads from side to side, but this hummingbird species has no irridescent gorget, auricular, or crown feathering that might be flashed by such movement, nor is the dull pinkish base of the mandible evident except at close range. No pronounced flicking of wings or tail occurred while singing.

Interactions between White-bellied Emeralds on the lek consisted of high speed chases through the forest mid-canopy, accompanied by rapid, chattering calls. Such chases were especially common immediately prior to dawn, when birds arrived in the area and presumably re-established ownership of specific display territories. Because we could not distinguish sexes, we are unable to exclude the possibility that some chases may have involved male–female interactions or males attempting to disrupt courtship activities elsewhere on the lek. However, in most cases birds returned

to their perch and resumed singing within seconds of initiating a chase, suggesting that most of these interactions represented defense of a display territory from intruding males. We were unable to determine whether visual or vocal cues generally caused a singing bird to leave its perch. We observed no copulations during more than 300 h of focused observations.

Life history and foraging ecology.—Little is known about the life history of the White-bellied Emerald. We found a single nest, containing two young, that was located 2 m above the ground on a small branch of a 2.6-m-tall *Guettarda Coombsii* sapling. One of the two juveniles present in this nest fledged on 4 March; three days later the empty nest was collected and is now deposited in the collection of the Western Foundation of Vertebrate Zoology. No leks were found within earshot of the nest site. E. Mallory (pers. comm.) noted a general decline in White-bellied Emerald singing activity in the Rio Bravo area between early February and mid-April 1990.

Nearly all White-bellied Emerald foraging activity occurred away from the leks. Birds occasionally hovered near their song perches and appeared to glean arthropods from nearby foliage; very few flowers were present within the general vicinity of the leks themselves. Several flowering *Trichospermum mexicanum* (Tiliaceae) trees were found in the Rio Bravo Conservation Area, and White-bellied Emeralds were consistently observed feeding at these trees. No leks were found within hearing distance of the *Trichospermum* trees, and no songs were given by the foraging birds. Although we saw Rufous-tailed Hummingbirds (*A. tzacatl*), White-necked Jacobins (*Florisuga mellivora*), and Wedge-tailed Sabrewings (*Campylopterus curvipennis*) feeding on flowers of *Lisianthus axillaris* (Gentianaceae) and *Pseudobombax septenatum* (Bombaceae), we did not observe White-bellied Emeralds regularly visiting these species.

Temporal variation in lek display.—Based on data collected during a single day from individual C1, there appears to be no significant temporal variation in song characteristics (Table 1). However, singing activity showed a definite temporal pattern that was similar among leks and among days (Fig. 2). On most days (excluding 19 February, see below), over 20% of the total songs given on a lek occurred during a 1-h period beginning immediately prior to sunrise ($\bar{x}$ = 22.6% [2.5], N = 5). Following this intense initial surge of singing activity, leks became virtually silent as all individuals left their display territories within an approximately 10-min period. Moderate levels of singing activity later resumed during mid-morning and continued through early afternoon; a secondary peak of song, more protracted but less intense than the early morning singing bout, occurred during the three hours preceding sunset.

Individuals sang more during intervals when larger numbers of birds

TABLE 1

TEMPORAL VARIATION IN SONG CHARACTERISTICS OF INDIVIDUAL C1 ON 10 MARCH 1990

	Song characteristics[a]					
Time	INTRO (kHz)	FREQ-I (kHz)	FREQ-II (kHz)	LAG (sec)	DELIVERY (number/sec)	PAIRS
06:00	6.99 (0.07)	8.81 (0.10)	7.21 (0.09)	0.108 (0.01)	0.42 (0.04)	3.35 (1.5)
06:50	6.98 (0.05)	8.78 (0.06)	7.14 (0.31)	0.108 (0.01)	0.39 (0.01)	3.43 (1.7)
09:50	6.95 (0.09)	8.70 (0.22)	7.22 (0.23)	0.113 (0.00)	0.40 (0.03)	3.30 (1.4)
13:30	7.03 (0.11)	8.75 (0.27)	7.11 (0.11)	0.111 (0.01)	0.43 (0.04)	3.47 (1.4)
16:20	6.99 (0.08)	8.74 (0.24)	6.99 (0.23)	0.118 (0.00)	0.53 (0.26)	3.94 (1.8)
P[b]	0.693	0.924	0.464	0.096	0.401	0.458

[a] Song characteristics as defined in Methods. Mean, with standard deviation provided in parentheses. Sample size (N) = 5 for all characteristics except PAIRS; for PAIRS, N = 43 (06:00), 60 (06:50), 37 (09:50), 53 (13:30), and 32 (16:20).
[b] Probability of differences among times based on nonparametric ANOVA.

were displaying on the lek (Lek A–N = 93 periods, Spearman rank correlation $r_s = 0.252$, $P = 0.015$; Lek B–N = 95, $r_s = 0.251$, $P = 0.014$; Lek C–N = 78, $r_s = 0.448$, $P = 0.0001$). Also, combining data from all three leks, there was a significant positive correlation between the number of 15-min periods an individual was present during the day and the mean number of songs it delivered during those periods of lek attendance (Fig. 3). That is, individuals that were consistently present on the lek sang more during their periods of attendance than did birds that were only sporadically present. However, we note that this relationship was not clear when each lek was analyzed separately (Lek A, $P = 0.642$; Lek B, $P = 0.048$; Lek C, $P = 0.251$), suggesting either a spurious correlation associated with the combined sample or failure to detect a pattern caused by smaller within-lek sample sizes.

Although patterns of activity were similar on five of the six days included in the analysis, behavior of Lek C was dramatically different on 19 February (Fig. 4). Approximately 55% of the total number of songs on this date were given during the first 30 min following sunrise, as compared to a mean of 18% on the other five days. Similarly, only 2080 songs were delivered on 19 February vs 6594 on the preceding day. The singing behavior of one bird (C2) had returned to a more typical pattern on 14 March (Fig. 4), and our subjective impression was that this was also true for other members of Lek C.

DISCUSSION

Bradbury (1981) listed three main characteristics of species that form leks. These included (1) absence of male parental care, (2) spatial clustering of displaying males within habitat that included no resources required by

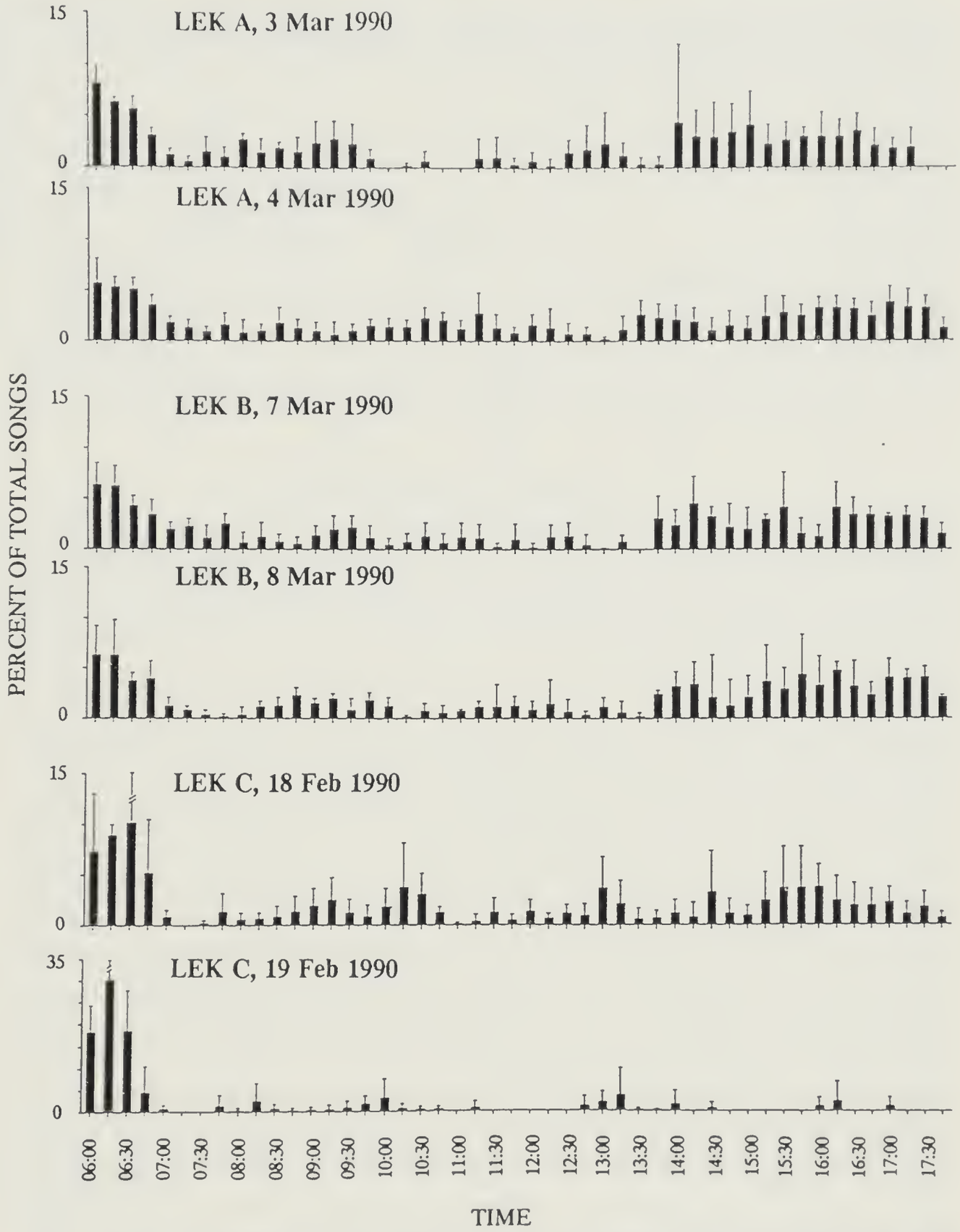

FIG. 2. Temporal distribution of singing activity in White-bellied Emerald leks. Each bar represents the mean percent of total songs occurring during a given 15-min period (+2 SE), based on standardized values for each individual in the lek (Lek A, N = 6; Lek B, N = 3; Lek C, N = 4).

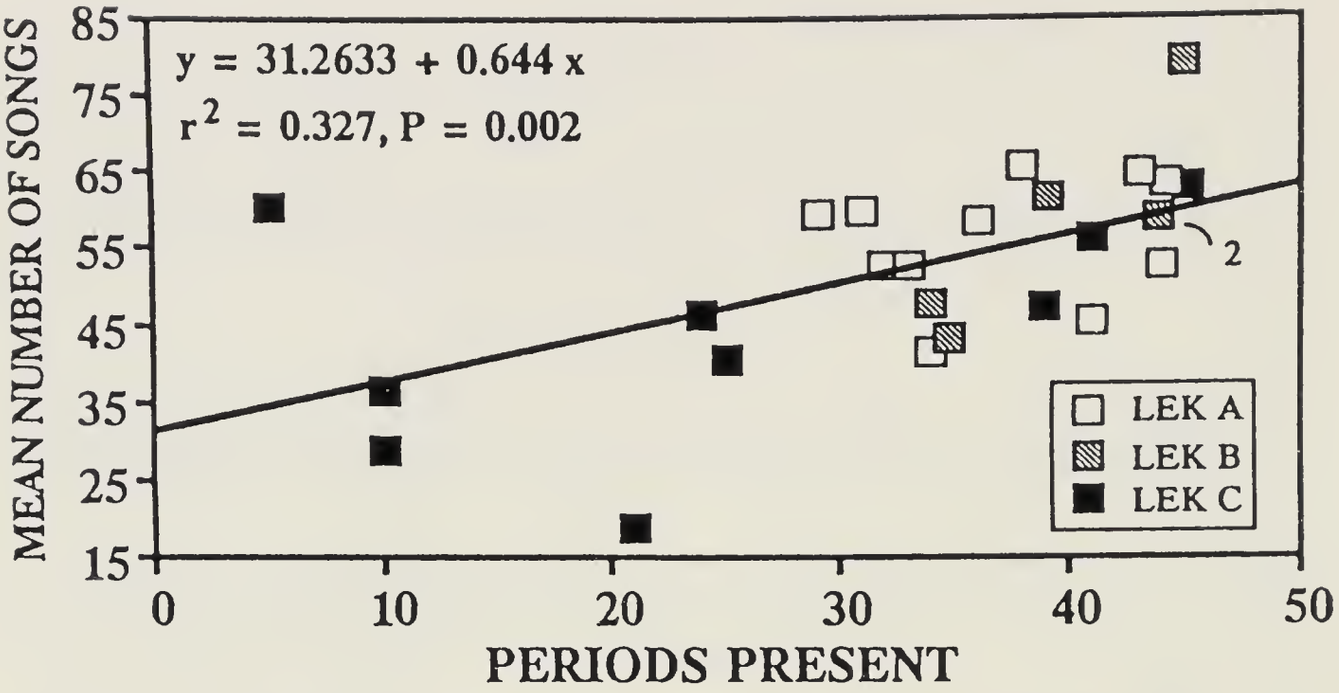

FIG. 3. Relationship between song delivery and lek attendance in White-bellied Emeralds. Mean number of songs given by each bird based on song counts during periods of attendance; "Periods Present" represents the total number of 15-min periods an individual was present during the day. Point labelled "2" represents exact coincidence of two data values at the given plot resolution.

females, other than the males themselves, and (3) ability of females to select a mate from a group of displaying males.

White-bellied Emeralds meet most, and probably all, of these criteria. In the majority of hummingbirds males do not participate in nesting or rearing of the young (Pitelka 1942), and we assume this to be the case with *A. candida*. White-bellied Emerald singing assemblies were spatially clustered, with no indication that this clumping was related to localized concentrations of food or other resources. Although the locations of singing assemblies may have been somewhat influenced by the slight forest gaps afforded by abandoned logging roads, White-bellied Emerald groups were clearly not uniformly distributed along these roads; furthermore, singing assemblies may have been found adjacent to abandoned roads simply because these trails were our almost sole means of access into the dense vegetation. Because we could not distinguish sexes of White-bellied Emeralds in the field, we can only assume that singing birds were males and that females visited assemblies for the purpose of selecting mates. However, the similarity of White-bellied Emerald behavior to that of several more thoroughly studied species of lekking *Phaethornis* hummingbirds (Snow 1968, Snow 1974, Stiles and Wolf 1979) suggests this is a reasonable assumption.

Few quantitative data have been presented regarding most aspects of

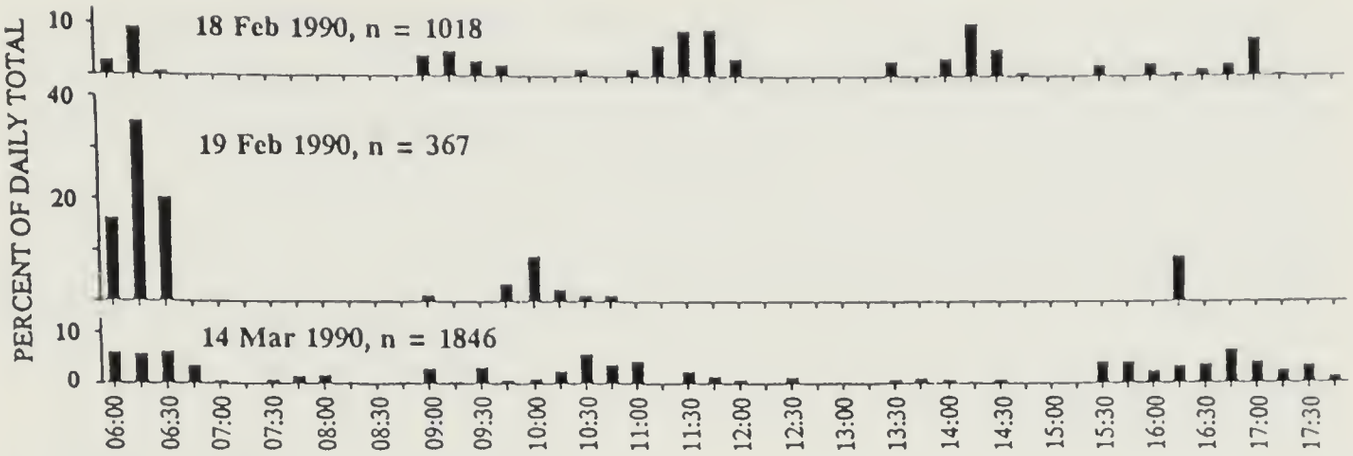

FIG. 4. Temporal patterns of singing by individual C2 on three dates. Each bar represents percent of total songs for indicated date occurring during a given 15-min period.

hummingbird lek behavior. White-bellied Emeralds and other described species of lekking hummingbirds are generally characterized by "exploded" lek systems (*sensu* Gilliard 1969), in which most displaying males are in audio contact with each other, but where direct visual interactions are limited or precluded by the combined effects of distance, terrain, or vegetation. Nearest neighbor distances between displaying White-bellied Emeralds varied from 14–32 m, with visual contact between adjacent individuals generally prevented by dense vegetation. Males displaying on presumed leks of the following species have been described as being separated by distances >15 m: Violet Sabrewing, *Campylopterus hemileucurus* (Skutch 1972); Blue-chested Hummingbird, *A. amabilis* (Skutch 1972); Rufous-tailed Hummingbird (Skutch 1981); Blue-throated Goldentail, *Hylocharis eliciae* (Skutch 1972); White-eared Hummingbird, *H. leucotis* (Skutch, in Bent 1940); Scaly-breasted Hummingbird, *Phaeochroa cuvierii* (Skutch 1964); and Violet-headed Hummingbird, *Klais guimeti* (Skutch 1958). Display territories in the genus *Phaethornis* (Long-tailed Hermit, *P. superciliosus*; Little Hermit, *P. longuemareus,* and Green Hermit, *P. guy*) may be separated by as little as 10 m (Wiley 1971, Snow 1974, Stiles and Wolf 1979), but visual contact between singing birds is, nonetheless, generally prevented by dense vegetation (Stiles and Wolf 1979).

The daily pattern of activity on White-bellied Emerald leks resembled that described for the Long-tailed Hermit (Stiles and Wolf 1979). In both species, an intense period of song and territorial defense began immediately prior to sunrise. About 1 h later, singing declined sharply as birds left the lek almost synchronously for what Stiles and Wolf (1979) termed a "breakfast break"; these authors found the timing of this break to coincide with the period of maximum nectar production in the flower

species used by Long-tailed Hermits. Moderate levels of song activity resumed after the "breakfast break" and continued through early afternoon; a secondary peak in singing, more protracted but less intense than the morning display period, characterized the hours prior to sunset. Stiles and Wolf (1979) hypothesized that these daily patterns of activity resulted from selective pressures associated with (1) the unpredictable appearance of females on the lek, (2) the recurring need to defend dominance and territory ownership, and (3) the optimal timing of foraging periods relative to food availability.

Activity patterns observed at Lek C on 19 February contrasted markedly with those seen on the previous days at this site and with patterns observed on four other days at Leks A and B. The cause of this anomaly, in which very few displays were given after the early morning "breakfast break," is uncertain. However, the night of 18 February was unusually cold (approximately 10°C), and we speculate that the approximately 3.7-g hummingbirds' metabolic reserves may have been depleted to such a point that most of the following day was devoted to foraging rather than display. Wetmore (1968) observed a similarly sized (3.1 g) tropical hummingbird (Garden Emerald, *Chlorostilbon assimilis*) that was immobilized under windy, 20.8°C conditions.

As in the 21 other species of Central American hummingbirds that are known or suspected to form leks (Table 2), song appears to be the primary form of advertising display used by White-bellied Emeralds. Skutch (in Bent 1940), noted that hummingbird courtship displays were either "static" (song delivered from a fixed perch) or "dynamic" (aerial flight displays). We know of no species of lekking hummingbirds that use courtship flight displays.

Based on our observations, and descriptions of *Phaethornis* lek behavior provided by Snow (1974) and Stiles and Wolf (1979), we postulate that persistent and vigorous singing may determine which individuals succeed in gaining copulations with visiting females. Song delivery by individual White-bellied Emeralds was greatest during those periods when maximum numbers of lek members were present. Furthermore, birds that consistently displayed throughout the day sang more, when present, than did individuals that were only sporadically present on the lek. We suspect that display frequency and intensity may define dominance relationships among displaying males or be used by females as cues by which to select mates. Unfortunately, observed copulations at hummingbird leks are typically rare (Stiles and Wolf 1979), making it virtually impossible to directly compare the actual reproductive success of different males.

Höglund and Lundberg (1987) and Höglund (1989) proposed that sexual differences in vocal displays might be substituted for plumage or size

TABLE 2
SEXUAL DIMORPHISM IN CENTRAL AMERICAN HUMMINGBIRDS KNOWN OR SUSPECTED TO FORM LEKS

Species	Source[a]	Plumage[b]	Size[c]
Band-tailed Barbthroat (*Threnetes ruckeri*)	7	M	S
Green Hermit (*Phaethornis guy*)	9	D	M
Long-tailed Hermit (*P. superciliosus*)	11	M	M
Little Hermit (*P. longuemareus*)	8	M	M
White-tipped Sicklebill (*Eutoxeres aquila*)	11	M	S
Scaly-breasted Hummingbird (*Phaeochroa cuvierii*)	5	M	M
Rufous Sabrewing (*Campylopterus rufus*)	7	S	M
Violet Sabrewing (*C. hemileucurus*)	6	D	S
Brown Violet-Ear (*Colibri delphinae*)	2	M	M
Violet-headed Hummingbird (*Klais guimeti*)	4	D	S
White-eared Hummingbird (*Hylocharis leucotis*)	3	D	S
Blue-throated Goldentail (*H. eliciae*)	7	S	S
White-bellied Emerald (*Amazilia candida*)	1	M	M
Blue-chested Hummingbird (*A. amabilis*)	7	D	S
Charming Hummingbird (*A. decora*)	10	D	M
Cinnamon Hummingbird (*A. rutila*)	10	M	M
Rufous-tailed Hummingbird (*A. tzacatl*)	7	S	S
White-tailed Emerald (*Elvira chionura*)	10	D	S
Coppery-headed Emerald (*E. cupreiceps*)	10	D	S
Snowcap (*Microchera albocoronata*)	10	D	M
Amethyst-throated Hummingbird (*Lampornis amethystinus*)	6	S	n/a
Wine-throated Hummingbird (*Atthis ellioti*)	7	D	n/a

[a] Presence of lek behavior based on following references: 1 = present study; 2 = ffrench (1980); 3 = Skutch, in Bent (1940); 4 = Skutch (1958); 5 = Skutch (1964); 6 = Skutch (1967); 7 = Skutch (1972); 8 = Snow (1968); 9 = Snow (1974); 10 = Stiles and Skutch (1989); 11 = Stiles and Wolf (1979).

[b] Plumage characteristics: D = dimorphic; S = slightly dimorphic; M = monomorphic. Based on descriptions provided by Ridgway (1911).

[c] Size characteristics: D = dimorphic (female : male wing length ratio ≤ 0.90); S = slightly dimorphic (ratio = 0.91–0.94); M = monomorphic (ratio ≥ 0.95). Based on measurements provided by Ridgway (1911); n/a = data not available for both sexes.

dimorphism in lekking birds. That is, vocalizations could serve as an alternative "target" on which selection could operate, thereby allowing monomorphism to persist even in the context of the strong sexual selection found in lek mating systems. Trail (1990) argued against Höglund's (1989) hypothesis, instead suggesting that monomorphism might evolve in lek systems where there was strong selection for females to share male morphological characteristics. However, Trail's (1990) arguments focused primarily on the existence of monomorphic lek species in which both sexes possess exaggerated plumage characters; little attention was given to the problem of drab, monomorphic lek birds such as the White-bellied Emerald.

Twelve of the 22 species (55%) of known or suspected lekking hummingbirds in Central America, including the White-bellied Emerald, are sexually monomorphic or only slightly dimorphic in plumage (Table 2). All of the 20 species for which measurements were available are sexually monomorphic in size, based on Trail's (1990) criterion of 10% difference in wing length; using Höglund's (1989) more restrictive cutoff of 5%, 10 species (50%) are monomorphic, and 10 (50%) are slightly dimorphic in size (Table 2).

Unfortunately, few careful studies have been made of the social behavior of known or suspected lekking hummingbirds, and many authors have failed to distinguish between resource-centered groups, such as occur near localized food sources, and leks (Pitelka 1942). For example, Skutch (in Bent 1940) described White-eared Hummingbirds as forming song assemblies that were spatially clustered in areas of uniform habitat and compared the functioning of these groups to manakin (Pipridae) leks; however, Stiles and Wolf (1979) thought this species "probably" exhibited food-centered mating territories. Barash (1972) described what he considered lek behavior in the Broad-tailed Hummingbird (*Selasphorus platycercus*), but did not specifically exclude the possibility of adjacent, food-centered mating territories. Stiles (1973) and Stiles and Wolf (1979) suggested that the normally non-lekking Anna's Hummingbird (*Calypte anna*) may switch from typical food-centered mating territories to a lek mating system, depending on the spatial dispersion of available nectar resources. Even for species in the fairly well-studied genus *Phaethornis,* it is somewhat unclear whether lek behavior may be abandoned under certain ecological conditions and replaced by resource-oriented mating strategies (Davis 1934; Oniki 1970; Stiles and Wolf 1979; L. Wolf, in Bradbury 1981).

Stiles and Wolf (1979) discussed the evolution of hummingbird lek behavior and sexual dimorphism in the context of foraging ecology. These authors concluded that "the critical determinant" of whether a species exhibits a lek social system or food-centered mating territory was "whether breeding males can control rich feeding areas which then serve as mating stations." Furthermore, Wolf (1969) and Stiles and Wolf (1979) suggested that sexual dimorphism in hummingbirds is often related to agonistic behaviors associated with defense of feeding sources; the monomorphic Long-tailed Hermit seldom exhibited intraspecific territoriality at flowers. Similarly, Bleiweiss (1985) hypothesized that the bright male-like plumage of females in some populations of the Tourmaline Sunangel (*Heliangelus exortis*) may reflect the results of nonsexual social competition for food.

The preliminary data presented here underscore the need for further study of monomorphic, lekking birds, including species such as the White-

bellied Emerald that lack exaggerated plumage characters. Available information is inadequate to address the relative merits of Höglund's (1989) behavioral transference hypothesis vs Trail's (1990) social selection hypothesis. Nonetheless, the intriguing diversity of mating and foraging systems exhibited within the Trochilidae, coupled with plumage characteristics that range from drab to extremely elaborate, suggest that behavioral studies focused on this family would provide valuable insights into sexual selection and the evolutionary basis of lek behavior.

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ROOSTING AND DIURNAL MOVEMENTS OF RADIO-TAGGED AMERICAN CROWS

PHILIP C. STOUFFER AND DONALD F. CACCAMISE[1]

ABSTRACT.—Cooperatively breeding birds characteristically defend territories in which they forage and roost all year. In contrast, the cooperatively breeding American Crow (*Corvus brachyrhynchos*) is notorious for large feeding and roosting aggregations during the non-breeding season. These observations suggest a pattern of fidelity to diurnal activity centers (DAC's) with daily movements to roosts and areas of superabundant food, much like the movements of communally roosting blackbirds and starlings. We radio tagged and color marked crows at a farm in central New Jersey to examine roost use and fidelity to territories during the winter. Birds exhibited two distinct movement patterns. Seven of 11 crows returned to the farm daily where they maintained stable territories in groups of 4–5. These "DAC-based" crows left the farm early in the afternoon and travelled to large communal roosts 14–18 km from the farm. The largest roost (>5000 crows) was 4.5 km from a landfill where thousands of crows fed daily. DAC-based birds sometimes stopped at landfills in transit to roosts. Although they were almost always together at the farm, crows from the same group usually did not travel together or make the same stops between the farm and the roost. In contrast to DAC-based crows, the other birds rarely returned to the farm and were difficult to find during the day. These "vagrant" crows were most often found at landfills and probably were not part of stable groups, although they used the same roosts as DAC-based birds. Vagrants disappeared during the middle of the winter, suggesting that they were not permanent residents in the study area. *Received 16 Oct. 1990, accepted 3 April 1991.*

American crows (*Corvus brachyrhynchos*) live in groups that breed cooperatively and defend year-round territories (Kilham 1984, 1989; Chamberlain-Auger et al. 1990; C. Caffrey, pers. comm., but see Good 1952). From these studies it appears that groups are stable seasonally, but most birds were not marked, so the extent of movement between groups is not known. Crows form large communal roosts (Davis 1894, Emlen 1938, Haase 1963), but the roosting patterns of marked individuals has not been examined. Thus it is not clear if crows remain faithful to stable diurnal activity centers (DAC's) but travel daily to distant feeding areas (DFA's) and roosts. Such a pattern is typical of communally roosting European Starlings (*Sturnus vulgaris*) and Common Grackles (*Quisculus quiscula*; Morrison and Caccamise 1985, 1990). Alternatively, crows in permanent groups may roost on their territories, and large roosts may be comprised of vagrant birds that range widely without fidelity to DAC's, as in Common Ravens (*C. corax,* Heinrich 1988). Large roosting aggregations of territory holders in cooperatively breeding species have not been reported.

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Groups in most cooperative species defend territories that contain all the resources necessary for the group (see discussion in Brown 1987, Chapter 2).

We investigated roosting and social organization in crows, using individually marked and radio-tagged birds. Our intent was to link diurnal observations of known individuals with use of roosts and distant feeding areas. We conducted the study in the winter because crows are known to roost communally then and because bird movements are not constrained by the need to tend eggs or nestlings. Specifically, we asked the following: are crow groups stable in the winter? If so, do individuals from groups use communal roosts? Do crows use DFA's in transit to and from roosts? Do groups remain associated at DFA's and roosts?

STUDY AREA AND METHODS

We studied crows using the agricultural fields at Rutgers Univ. in New Brunswick, New Jersey. The farm has approximately 2 km^2 of horse pastures, turf, corn, and vegetable fields. It is bordered by a suburban residential area to the east and south, Rutgers Univ. campus to the north, and the expansive lawns of several corporate complexes to the west. Small woodlots rim the farm except to the west.

Crows foraged in the pastures and harvested fields at the farm. We captured foraging crows by baiting with chicken eggs dosed with the sedative alpha-chloralose (Stouffer and Caccamise, in press). We kept sedated crows overnight to allow them to recover (Stouffer and Caccamise, in press). We outfitted crows with radio transmitter packages mounted with backpacks (Morrison and Caccamise 1985). The total weight of the transmitter package was 8–15 g, less than 3% of body mass. Although the transmitter and battery combinations that we used had effective ranges of up to 6 km and expected lives of 4–6 months, their effectiveness in the field was determined by the extent to which the birds damaged their antennas (see below). In addition to radio-tagging, we also bleached a pattern on the primaries or secondaries of each bird so we could visually identify individuals (White et al. 1980).

We attempted to locate each crow during the daylight hours 4–5 days a week from the time of capture through the end of March. For DAC-based birds (see below), one location sample was taken each day at a random time during the period that crows used the farm (about 08:00–13:00 h EST). We located birds at night 3–4 times a week by checking known roosts or by following bearings of birds as they left the farm. We attempted to find birds at DFA's by following bearings of birds as they arrived and departed from the farm and the roost, or by checking sites known to have been used by crows from the same roosts.

We quantified the activity of crows at the farm by continuously sampling focal individuals for three minute intervals (Altmann 1974). These data were entered on a portable computer in the field. We subsampled the data at 30 second intervals to generate discreet, independent samples. For this analysis, behaviors were combined into four categories: forage, which included walking with head down as well as handling food items; perch, including preening as well as terrestrial and arboreal perching; locomotor, which included walking with head up and flying; and other, primarily vocalizing and social interactions.

RESULTS

We captured 13 crows from 6 November through 15 February (Table 1). All were over one year old (AHY/ASY: Pyle et al. 1987). Crows

captured on 17 December, 6 February, and 15 February were part of groups that we had observed for several days before capture, and which we suspected to be stable groups of permanent residents of the farm. Radio-tagged birds from these groups returned to the farm nearly every day and are referred to as DAC-based crows (see below). The birds captured on 6 November and 16 January did not regularly return to the farm and did not remain in stable groups. These birds are referred to as vagrant crows (see below).

Two crows are not included in Table 1 nor in any subsequent results. The first bird, captured on 16 January, was found dead near the farm on 18 January. From the remains, we could not determine if it was killed by a predator or dismembered by scavengers. The second bird had massive damage to primaries and secondaries on both wings when it was captured on 15 February. This bird probably was a member of the group captured that day, since we had repeatedly noticed a bird with damaged feathers in the same area. We attached a transmitter, but we did not locate the bird again.

Territories of DAC-based crows.—DAC-based crows returned to the farm nearly every day throughout the winter. We successfully located these seven birds at the farm on 88.6% of attempts (242 of 273). Because they were often foraging in fields or perched at the periphery of fields, we usually located birds visually. It was necessary to use radio signals to find birds when they ranged deeper into woodlots or into residential areas. We relied almost entirely on visual locations for birds 13 and 15; both birds damaged their antennas, drastically reducing transmitter range. The signals from these birds became increasingly poor until they could not be received at all by two weeks after release. The other birds also damaged their antennas, but we could still receive weak signals.

Plots of daily locations show that territories of DAC-based birds overlapped only slightly (Fig. 1). Based on a minimum convex polygon estimate (e.g., Anderson and Rongstad 1989), territory sizes were 0.26 to 0.49 km^2 (group A = 0.49 km^2, B = 0.38 km^2, C = 0.26 km^2), although groups B and C used additional areas to the north where we were unable to follow and delineate territorial boundaries. We usually observed five individuals in each group, but at times we were unable to see all members at once. Birds from adjacent territories often foraged 50–100 m apart in the same fields, but we saw no disputes at territorial boundaries until late March. On four occasions, one or two apparently vagrant crows foraged in the same fields with territorial birds, but we never saw these birds chased away by residents. The territories of groups A and C overlapped slightly near the intersection of the lake and Ryder's Lane (Fig. 1); twice we saw chases between the two groups in this area.

TABLE 1

CAPTURE DATES AND GROUP SIZES AT THE TIME OF CAPTURE OF RADIO-TAGGED CROWS. DAC-BASED CROWS WERE MEMBERS OF TERRITORIAL GROUPS AT THE FARM; VAGRANT BIRDS WERE NOT (SEE TEXT)

Capture date	Bird number[a]	Group size	Territorial status	Group
6 November	1	>100	Vagrant	—
	2	>100	Vagrant	—
17 December	4	5	DAC-based	A
	5	5	DAC-based	A
	6	5	DAC-based	A
16 January	7	>7	Vagrant	—
	8	>7	Vagrant	—
6 February	11	5	DAC-based	B
	12	5	DAC-based	B
15 February	13	5	DAC-based	C
	15	5	DAC-based	C

[a] Bird numbers correspond to the last two digits of the USFWS series beginning with 685-65101.

One bird switched groups for a few days but later returned to its original group. Bird 5 was with birds 4 and 6 in group A 91% of the times it was found, but we also located it in a second, adjacent territory (the four points north of Rt. 1 in Fig. 1). Although bird 5 foraged and perched within a few meters of the two crows in the adjacent territory, we saw no aggression directed toward it.

Activity varied slightly over the course of the day while crows were at the farm (Fig. 2). Perching was the most common activity for most of the day, accounting for 29 to 66 percent of hourly observations. Locomotor activity varied between 17 and 43 percent. Both perch and locomotor varied significantly among hours, probably as a result of the high frequency of perching at the expense of locomotor at 1300 and 1400 h (log-likelihood test, both $G > 19.9$, $df = 6$, both $P < 0.003$). Time spent foraging remained relatively constant between 15 and 21 percent. The apparent decrease in foraging as the day progressed was not significant by regression ($R^2 = 0.47$, $P = 0.09$).

Roosting by DAC-based crows.—By the second night after release all DAC-based crows joined communal roosts. Until late December most birds used a roost in Perth Amboy about 14 km NE of the farm. This roost had a maximum of about 500 crows through December but was abandoned by 12 January. For the rest of the winter, all locations of roosting birds were from a roost on Staten Island, about 18 km ENE of the farm. This roost contained at least 5000 birds through the end of March. Both roosts were in secondary forest dominated by red maples

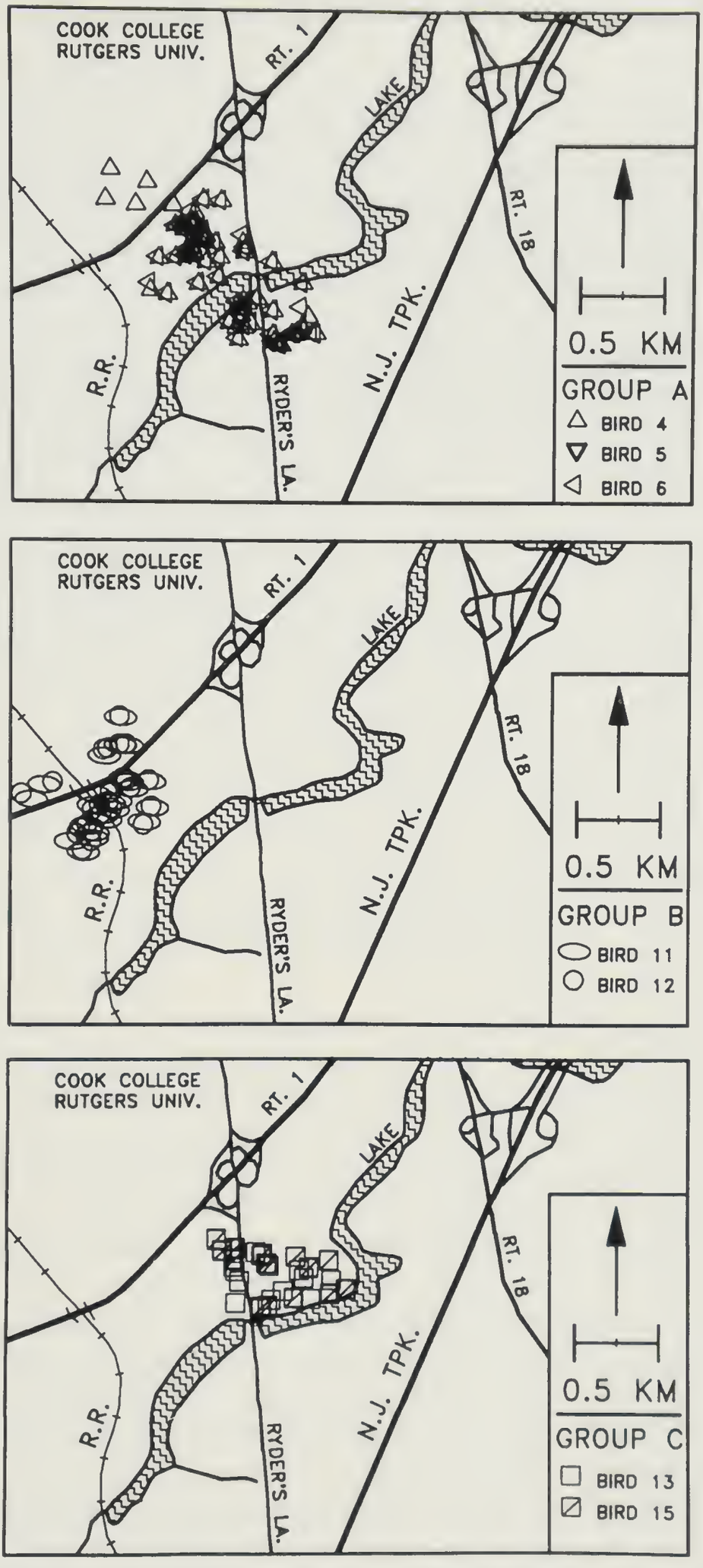

FIG. 1. Territories of DAC-based crows. Plots show daily locations of marked individuals from the indicated groups.

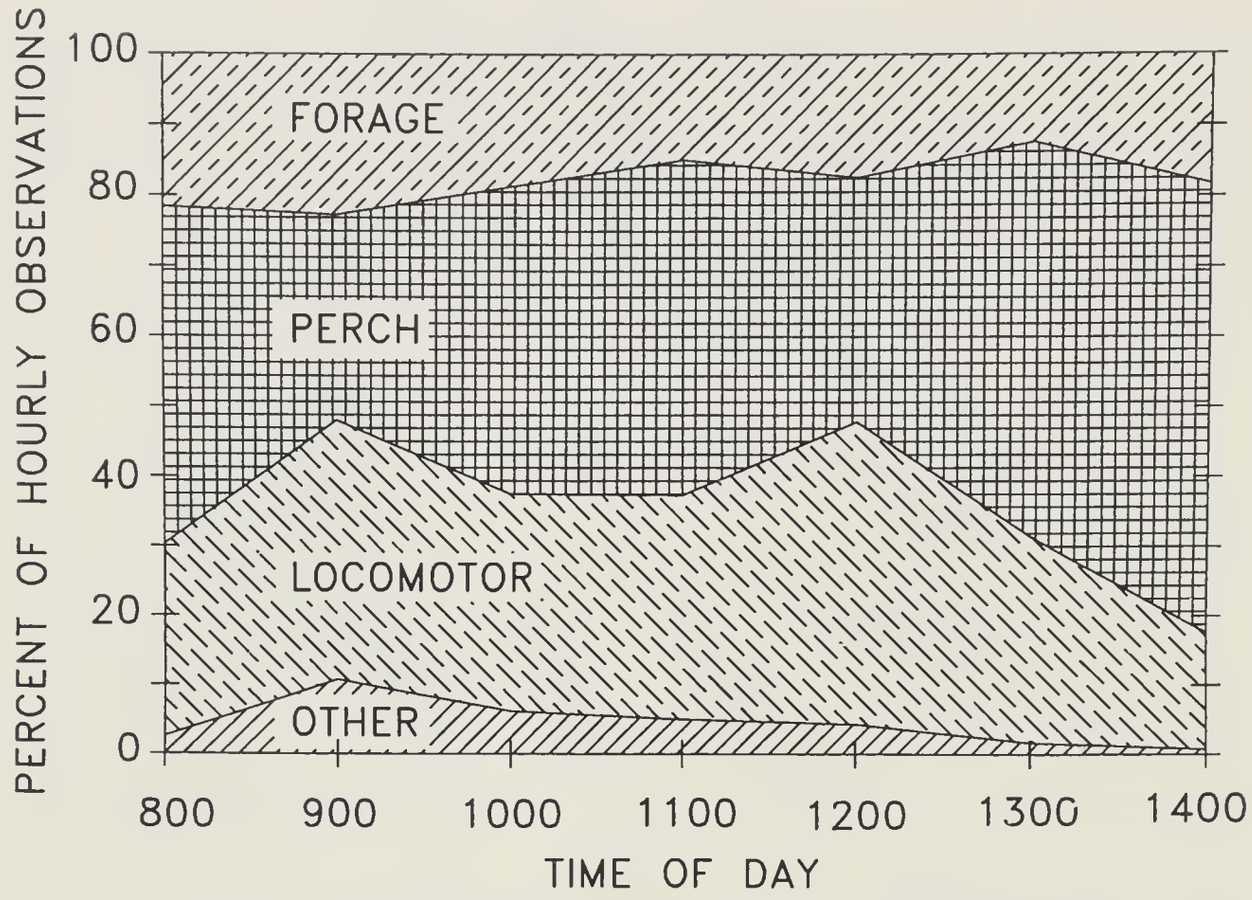

FIG. 2. Activity budget of DAC-based crows on their territories.

(*Acer rubrum*) 3–8 m tall. In addition to American Crows, a smaller number of Fish Crows (*C. ossifragus*) used the roosts. Crows usually assembled at several locations within 0.5 km of the roost site, then coalesced at the roost by dusk.

Six of the seven DAC-based crows roosted at the farm on the night they were released. Birds 4, 5, and 6 roosted together in a tall white spruce (*Picea glauca*). Birds 11, 13, and 14 roosted in woodlots but could not be precisely located. None of the DAC-based crows roosted at the farm after the first night, although we did observe DAC-based birds roosting at the farm in April, after the conclusion of this study.

We successfully located DAC-based birds at communal roosts on 84.1% (122 of 145) of attempts. Some absences were probably related to weather. January 25 was rainy and foggy, and no DAC-based birds used a communal roost, although they did leave their territories. Other absences may have been due to poor radio performance; the Staten Island roost was sufficiently spread out that we may not have been close enough to detect the weak signals from some birds.

Travel to roosts by DAC-based crows.—Our measurements of commuting time between the farm and roosts indicated that birds stopped in transit. Stops were shorter in the morning than in the afternoon. Birds left the roost between 06:17 and 07:10 h and arrived at the farm between

07:10 and 07:54 (Fig. 3). They remained on their territories until 13:00 to 14:40, and arrived at roosts between 15:39 and 17:08. Based on an average body mass of 521 g, we calculated the velocity of maximum range for our birds to be 51 km-h^{-1} (Caccamise and Hedin 1985). Thus the commute to the Perth Amboy roost (14 km) should have taken 16 min and 21 min to the Staten Island roost (18 km). There was only a 50 min difference between mean departure time and mean arrival time in the morning, leaving about 30 min for a stop. In the afternoon, however, the 135 min difference between mean departure time from the farm and mean arrival time at the roost allowed at least 100 min for a stop.

On 11 occasions we found DAC-based birds at a landfill in Edison about 4 km from the farm between the farm and both communal roosts. We found two DAC-based crows at the Edison landfill in the morning. They continued on to the farm before we returned by 07:50 and 08:05. On nine other occasions we found DAC-based crows at the same landfill between 13:30 and 16:20. These birds were present at roosts the same evening. We never found DAC-based birds at landfills between 08:05 and 13:30, the period when we were searching for vagrants (see below).

Based on counts of birds flying into and out of landfills, hundreds of crows at a time used the Edison landfill, and thousands used a giant landfill on Staten Island north of the roost. We never located DAC-based birds at the Staten Island landfill, but it was logistically difficult to find birds there. There were several good vantage points from which to watch birds and receive signals near Edison, but most of the giant complex on Staten Island was inaccessible.

Crows from the same group rarely travelled together between the farm and the roost, and in some cases even used different roosts, although they were nearly always together at the farm. Birds in the same group arrived at or departed from the farm or the roost within two minutes of each other in only 29% (2 of 7) of observations in which we knew exact arrival or departure times. Similarly, on only 11% (1 of 9) of observations of DAC-based birds at landfills did we find more than one bird from the same group.

Vagrant crows.—We saw behavioral differences between vagrants and DAC-based crows beginning before the birds were captured. Birds 1 and 2 were captured together at the farm on 6 November as a part of a group of about 150 crows foraging in a recently harvested corn field. The birds in that group fought over access to the eggs we provided, and birds had to pick up the eggs and fly away in order to avoid harassment. The group of vagrants from which birds 7 and 8 were captured did not fight over eggs, although seven birds were eating the eggs at the same time. Other crows vocalized from nearby trees, but those birds may have been the

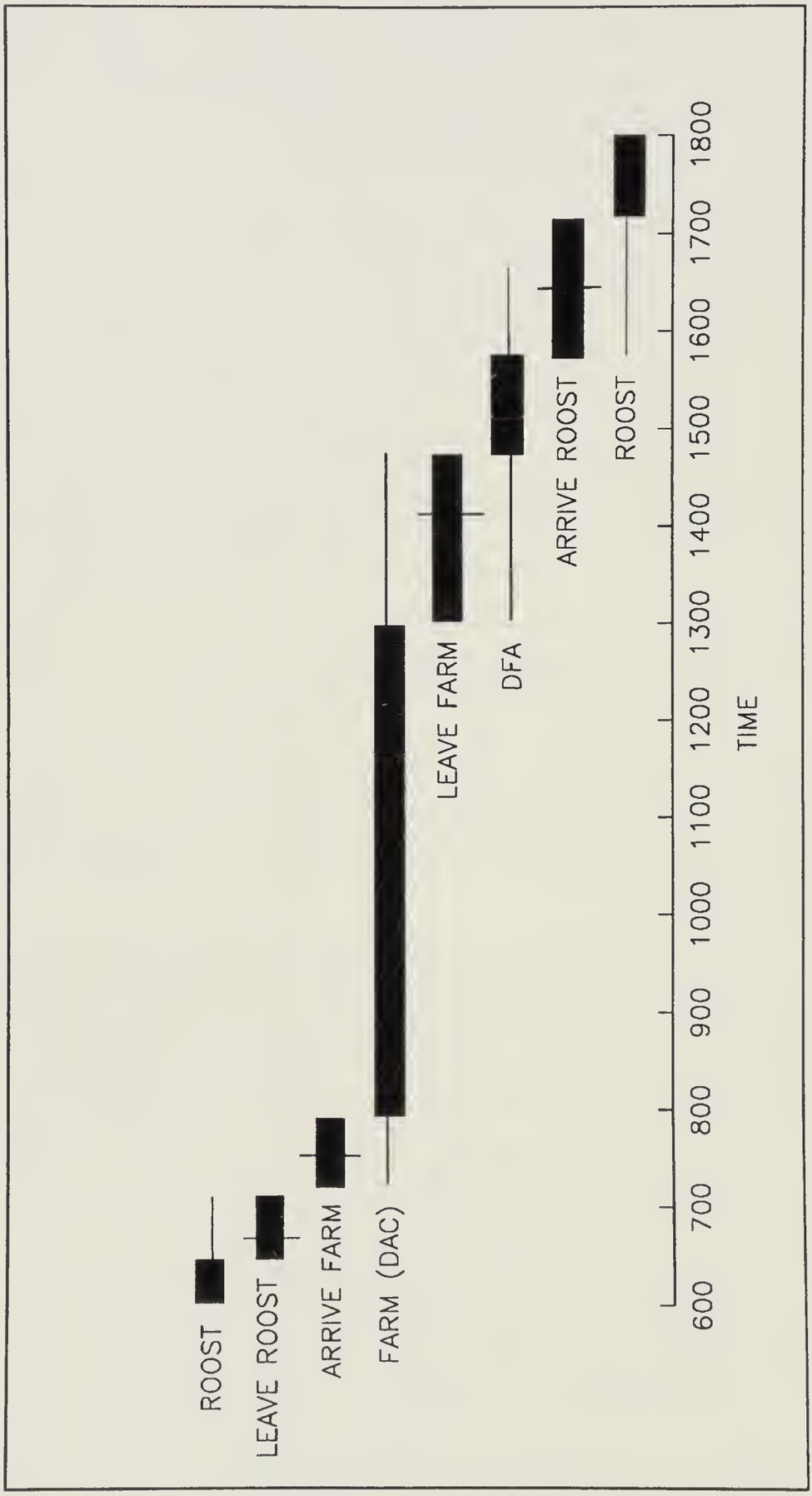

FIG. 3. Pattern of daily movement for DAC-based crows using distant feeding areas (DFA's) and communal roosts. For arrival and departure times, horizontal bars show ranges and vertical lines show means. For roost, farm, and DFA, horizontal lines show ranges and horizontal bars show times when birds were most likely to be present.

residents that we later captured at the same site. We also saw conflict over food at landfills and at roosts. In contrast, DAC-based birds took turns eating eggs, with two or three eating at a time while the others perched nearby on the ground or in trees. The first group to eat would then move off to the side and other individuals would descend, although it was not unusual for at least one member not to eat eggs at all.

The four vagrants were not faithful to the farm or to the individuals with whom they were captured. For example, bird 1 returned to the farm in a large flock four times, then switched to the Edison landfill. Bird 2 did not return to the farm, but was twice located at the Edison landfill, and later began to leave the roost in the direction of the Staten Island landfill. In general, vagrants were very difficult to locate during the day, although they used the same roosts as DAC-based birds. We spent over 90 hours searching the study area for diurnal locations of vagrants, but we only found them on 31.8% (21 of 66) of attempts. We stopped systematically searching for these birds during the day after they disappeared permanently from communal roosts.

Vagrants used communal roosts at Perth Amboy and Staten Island, but each disappeared permanently from roosts during the winter. Bird 1 was last located on 23 November, bird 2 on 2 January, bird 7 on 9 February, and bird 8 on 2 March. Before they disappeared permanently, we located roosting vagrants on 70.7% (41 of 58) of attempts. In addition to using communal roosts, on five nights bird 1 roosted, apparently alone, in a stand of white pines (*Pinus strobus*) 8 km NNE of the farm.

DISCUSSION

DAC-based crows.—The territorial fidelity and stability of DAC-based groups at the farm was much like that reported by Kilham (1984, 1989) from Florida and Chamberlain-Auger et al. (1990) from Cape Cod, although Good (1952) reported that crows were only territorial in the breeding season in Ohio. The groups we studied probably bred at the farm beginning in April; we saw members of each group carrying nesting material at that time. Because we only marked two or three birds in each group, we cannot be certain that the other group members were the same individuals throughout the winter, but since we saw considerable social interaction without conflicts within the groups, we suspect that groups were stable. The birds we captured were all AHY/ASY, so we cannot evaluate possible behavioral differences as a function of age.

Bird 5 divided its time between group A and a second, adjacent group, possibly in an effort to join the second group. The second group had only two other individuals, compared to four others in group A, so there may have been a better chance to breed by joining a smaller group. Similar

short-term dispersal forays are common in Florida Scrub Jays (*Aphelocoma c. coerulescens*; Woolfenden and Fitzpatrick 1984:151, see also Brown 1987:104).

Daily movements of DAC-based crows, which included daily return to a group territory, use of supplemental food sources off the territory, and roosting communally is an unusual pattern for a cooperatively breeding species. Typically, cooperative species maintain family territories during the non-breeding season on which they forage and roost (e.g., Brown 1978). In several species, adjacent breeding groups combine in the non-breeding season, and the resulting larger group ranges over the area of all the smaller breeding territories (Long-tailed Tit [*Aegithalos caudatus*], Gaston 1973; Buff-rumped Thornbill [*Acanthiza reguloides*], and Striated Thornbill [*A. lineata*], Bell and Ford 1986). White-winged Choughs (*Corcorax melanorhamphos*) wander, as a group, over a wide area in the non-breeding season, foraging largely on grain stubble (Rowley 1977). Scrub Jays make short forays out of their territories to forage on grain handouts, but return promptly (Woolfenden and Fitzpatrick 1977). We know of no other cooperative species with the pattern displayed by crows, in which groups associate for part of every day and then break up to forage and roost elsewhere.

Use of supplemental food sources, especially landfills, off their territories may permit DAC-based crows to maintain their territories at times when the territories do not provide sufficient food. We believe, however, that the crows we observed were seldom food limited on their territories since they spent relatively little time foraging and most of the day loafing (Fig. 2). Further, they often cached food and they became less attracted to baits over the course of the day. We consider it more likely that crows used food sources off their territories because either (1) foraging was more efficient or safer at DFA's, or, (2) visiting supplemental sites enabled birds to know of foraging sites in the event that they were unable to find food on their DAC's, such as after a heavy snow.

It is interesting that groups did not remain together except at the farm. This suggests that the advantage to individuals of maintaining groups on territories does not persist when not on the territory. Further, this means that birds that use the same DFA or roost are essentially anonymous to each other in comparison to birds that are together during the day. This anonymity may explain why crows share food on their territories (see also Kilham 1989:22) but fight over food off their territories. Within groups, restraint from eating (or food sharing; see Taylor and McGuire 1988) may be a cooperative act maintained by a high potential for future interactions. At large roosts or DFA's, however, there is little chance to interact repeatedly with the same individuals, making reciprocity less likely (Trivers

1971, Axelrod and Hamilton 1981). Food sharing may also be important for forming and maintaining the social bonds necessary for successful cooperative breeding (see discussion in Seyfarth and Cheney 1988).

Vagrant crows.—Movements of vagrant crows differed from those of DAC-based crows in four respects. (1) Vagrants left the area in the middle of the winter. (2) Vagrants probably did not have DAC's. They were not faithful to the farm or any other location and were most likely to be found at landfills. (3) Vagrants and DAC-based birds differed temporally in their use of landfills. DAC-based birds seldom or never used landfills in the middle of the day (between 08:00 and 13:30, Fig. 3), but vagrants used landfills at all hours. (4) Vagrants that were captured together did not remain together.

These patterns of diurnal movement and short-term residency in the study area suggest that vagrants may be migrants from farther north. Alternatively, they may be birds that dispersed from local natal groups but have not found new groups. We think the radio-tagged vagrants were migrants, since they were over one year old and they disappeared in midwinter. A similar pattern of irregular movement followed by disappearance was reported for vagrant Common Ravens (Heinrich 1988). Kilham (1989:44) also reported wandering flocks of vagrant crows in Florida during January. Movement patterns of vagrants differ in scale from movement within a smaller area by "floaters" in territorial species (e.g., Smith 1978). Also, vagrant crows did not form any temporary associations with stable groups, as do floaters (Smith 1978).

Roosting.—All crows used communal roosts throughout the winter. Most absences were from March, suggesting that some crows used another, undiscovered roost during that time. Based on visual observations after all radios had expired, DAC-based birds began roosting at the farm in April. Seasonal variation in roost choice is also common in starlings (Morrison and Caccamise 1985).

Crow roosts were spatially associated with superabundant food sources, as appears to be the case for roosts of other species (Caccamise and Morrison 1988). A recent explanation for communal roosting behavior, the "patch-sitting hypothesis," suggests that large roosts form as passive aggregations near superabundant food supplies (Caccamise and Morrison 1986). The largest and longest-lasting roost, on Staten Island, was near an enormous landfill used by thousands of crows. It would be interesting to examine if roost establishment follows landfill establishment on a broad geographic and temporal scale; Davis (1894) reported that "able bodied crows do not roost on Staten Island in winter, but fly as night approaches to better protected retreats in New Jersey." This is the reverse of the pattern a century later, after Staten Island became a dumping ground for

the other boroughs of New York City and former agricultural land in New Jersey was replaced by urban sprawl.

For vagrants, roosting on Staten Island reduced the commute to the Staten Island landfill to only 4.5 km, supporting the patch-sitting hypothesis for roost establishment (Caccamise and Morrison 1986, 1988). Finding DAC-based crows at the Staten Island landfill would have provided support for the patch-sitting hypothesis for those birds. DAC-based crows stopped at the Edison landfill before continuing on to the Perth Amboy or Staten Island roosts, and we suspect that they also used the Staten Island landfill, although we were unable to find them there.

Roost-site selection by crows that did not use large roosts provides a comparison to the typical communal roosting pattern. Characteristics of roosts used by these crows suggest that they chose roost sites to avoid detection by predators or to reduce heat loss, but neither of these advantages was likely at large communal roosts. Birds 4, 5, and 6 roosted together in the dense cover of a spruce for one night after release. Bird 1 roosted repeatedly in a pine. We also saw birds 11 and 12 and several unidentified birds (probably the rest of group B) roost in a Norway spruce (*Picea abies*) in May. Predation deterrence is probably the greatest benefit to crows roosting in foliage, especially in May (Walsberg and King 1980). Cooperative groups in other species have been reported to roost together, huddled deep in foliage, on their territory (e.g., White-winged Chough, Rowley 1977; Buff-rumped Thornbill, Bell and Ford 1986; Green Wood-Hoopoe [*Phoeniculus purpureus*], Ligon et al. 1988).

Several crows roosting in dense foliage is a dramatic contrast to thousands of birds blanketing a woodlot of scrubby trees that offer no cover, such as at the Perth Amboy or Staten Island roosts. Since birds at large roosts space themselves out and do not seek cover, it is unlikely that these roost sites provide any thermal benefit (see also Kelty and Lustick 1977, Walsberg 1986). Although large roosts have the advantage of diffusion of risk and many eyes to spot predators (Crook 1965, Pulliam 1973), these roosts are probably easily detected by predators (see discussion in Skutch 1989, Chapter 4). Presumably the risk of a predator finding the roost is outweighed by the benefits of being in a large group.

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POPULATION DYNAMICS OF BLUE JAYS AT A BIRD FEEDER

MARGARET B. HICKEY[1] AND MARGARET CLARK BRITTINGHAM[2]

ABSTRACT.—Hickey color banded and monitored 2373 Blue Jays (*Cyanocitta cristata*) from 1953 until 1976 at her bird-feeder in Madison, Wisconsin. The mean annual survival rate of Blue Jays calculated from reobservation and recapture data by the Jolly-Seber method was 0.54. The annual survival rates of juvenile and adult jays calculated from band returns by the life table approach were 0.45 and 0.53, respectively. Forty-three Blue Jays lived to be at least seven years old, and the oldest Blue Jay reported was a 14-year-old mated male.

The abundance of Blue Jays fluctuated seasonally and annually. Peak numbers occurred during the breeding season ($\bar{x}$ = 99.0 individuals) after young fledged, and low numbers occurred during the non-breeding season ($\bar{x}$ = 21.3 individuals). The annual abundance of Blue Jays was not correlated with abundance of acorn mast.

Blue Jay populations increased between 1953 and 1976, but changes in numbers were not correlated with local changes in survival rates, rates of reproduction, or changes in migratory behavior. The data are most consistent with the hypothesis that regional changes in survival rates occurred during this time period, and these changes were then reflected in a local increase in the abundance of Blue Jays. *Received 11 Dec. 1990, accepted 9 April 1991.*

Long-term studies of marked individuals are valuable for estimating survival rates and longevity, detecting changes in abundance of bird populations, distinguishing long-term population trends from normal year-to-year fluctuations in numbers, and determining the underlying causes of population fluctuations. The Blue Jay (*Cyanocitta cristata*) is a common species throughout eastern North America, yet relatively little is known about its population dynamics, particularly in comparison to other jays such as the Florida Scrub Jay (*Aphelocoma coerulescens*) (Woolfenden and Fitzpatrick 1984). In this paper, we report results of a banding study of Blue Jays conducted from 1953 until 1976 in Madison, Wisconsin. Specifically, we report on survival rates, longevity, and causes of mortality, and we address the following questions: (1) Do Blue Jay populations fluctuate within and between years? (2) Are fluctuations in numbers of Blue Jays correlated with changes in acorn mast abundance? (3) Did the abundance of Blue Jays remain the same during the 23 years of the study? and (4) Can changes in numbers of Blue Jays be correlated with changes in survival rates, reproductive rates or migratory behavior?

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TABLE 1

AGE AND SEX OF BLUE JAYS BANDED AT THE HICKEY STUDY SITE, MADISON, WISCONSIN, 1953–1976

Age[a]	Sex		
	Female	Male	Unknown
HY	186	113	943
AHY	154	52	246
UNK	120	55	504
Total	460	220	1693

[a] Hatching year (HY), after hatching year (AHY), unknown (UNK).

METHODS

Study area.—From January 1953 through August 1976, Hickey banded and monitored Blue Jays at her bird feeders. All banding was conducted in the side yard of the Hickey home on the southwest side of Madison, Wisconsin. The yard was approximately 0.2 ha and was on the edge of a mature oak (*Quercus* spp.) and hickory (*Carya* spp.) woodlot about 0.1 km × 1.5 km. The woodlot and surrounding pasture were converted to residential development beginning in the early 1950s and became a mix of lawns, woods, and houses. Between 1953 and 1976, the study area and surrounding residential neighborhood did not change significantly.

Capture and marking.—Blue Jays were captured with funnel traps baited with corn and sunflower seeds and with a platform feeder modified to function as a trap. The traps were opened and baited on a year-round basis whenever an unmarked Blue Jay was observed in the yard. The traps were kept open until all Blue Jays were banded. Most unbanded jays were captured and marked within a day or two of arriving in the yard, and approximately 90% of the Blue Jays frequenting the yard were marked at all times (J. J. Hickey, pers. comm.).

During the 23 years of the study, the only extended period when no marking or sighting occurred was from February–August 1964, when the Hickey family was out of the country. This period has been deleted from the analysis. In other years, there were only occasional months when no data were collected. These months have also been deleted from the analysis. During this study, 2373 Blue Jays were captured a total of 3065 times. Each bird captured was banded with an aluminum U.S. Fish and Wildlife Service band and given a unique combination of color bands. After a number of years, the aluminum bands became thin and worn, so older birds were routinely banded with a new FWS band when they were recaptured. Females captured during the breeding season were sexed by the presence of a brood patch. The sex of all other jays was initially reported as unknown. During the breeding season males were identified when mated to a known female (Table 1).

Determination of age and age ratios.—The ages of Blue Jays captured between 1 June and 31 December were determined by plumage characteristics and color of the mouth lining and recorded as hatching year (HY) or after hatching year (AHY). All jays captured between 1 January and 31 May were recorded as age unknown. For purposes of analysis, each bird was considered to become one year older on 1 June.

For each year, we calculated the ratio of banded juvenile (HY) to adult (AHY) Blue Jays captured or sighted on the study site during the breeding season and fall migration period. Regression analysis was used to test for trends in age ratios during these time periods.

Sightings and band returns.—Sightings of marked birds were recorded daily whenever jays were observed in the Hickey yard. In addition, many of the neighbors also reported sightings of marked birds. A total of 8318 observations of 1599 Blue Jays were reported. Seven hundred seventy-four birds were not observed after the month they were banded. Band returns were used to determine causes of mortality and the migration route.

Population analysis.—The calender year was divided into four seasons corresponding to different periods in the life cycle of the Blue Jay. Divisions into seasons were based on other studies of the Blue Jay and on an examination of the trapping data from this study.

Spring migration was defined as April and May. This is the time period when migrations of Blue Jays have been reported in the Madison area (Schorger 1961, 1964). In this study, the number of new Blue Jays captured rises sharply during April and May, suggesting that new birds are moving through the area (Table 2). At the same time migrants are moving through, many resident birds are nest building and incubating eggs (Bent 1946).

The breeding season was defined as June and July. During this period, some Blue Jays are still incubating eggs, but many others have fledged young (Bent 1946). Post-breeding flocks composed of many family groups are starting to form (Hardy 1961). In this study, fledged young were first captured and banded during June and July (Table 2).

The fall migration period was defined as August and September. The timing and magnitude of fall migration appears to be highly variable. Flocks of migrating Blue Jays have been reported occurring any time from August until the middle of November (Broun 1941, Bent 1946, Middleton 1974). We did not include October and November in the migratory period because few new birds were marked during these months (Table 2). In addition, the majority of banded birds recorded in October were resident throughout the winter.

The remainder of the year (October through March) was defined as the non-breeding season. During this period, stable flocks form that remain loosely associated throughout the winter (Hardy 1961, Racine and Thompson 1983). In our study, few new jays were banded during this period (Table 2).

For each season and year, the total number of jays reported was tallied, and the average number of Blue Jays present per season for all years combined was calculated. Analysis of variance was used to test for differences among means, and a Tukey test ($\alpha = 0.05$) was used to determine which means were different.

The total numbers of jays reported each season and year were tallied and regression analysis was used to test for population trends. For each regression equation, we conducted the Durbin-Watson test for autocorrelation; where the error terms were autocorrelated, the iterative approach was used to transform autocorrelated variables, and the models were re-run (Neter et al. 1985). No models showed autocorrelation after the first iteration.

In order to determine whether the numbers of jays reported at the Hickey study site were representative of population fluctuations occurring in the Madison area, the numbers of jays reported at the Hickey site each December were plotted against the number of Blue Jays reported per party hour on Audubon Christmas Bird Counts in Madison, Wisconsin, during the same years (1953–1975). The correlation coefficient (r) was calculated, and residuals were plotted and examined to ensure that the model was appropriate (Box et al. 1978).

Assessment of mast abundance.—Between 1953 and 1969, the Wisconsin Conservation Dept. (Wisconsin Dept. of Natural Resources) conducted an annual mast and berry production survey. The state was divided into five districts based on geographic location, and acorn production was reported as the percentage of "best conceivable crop" or percentage of full crop. We calculated the Spearman rank correlation coefficients to test whether numbers of Blue Jays present during the non-breeding season were correlated with acorn mast abundance in southern Wisconsin. We also calculated the Spearman rank correlation coefficient between statewide acorn abundance and number of jays present during the fall migration period.

TABLE 2

NUMBER OF FIRST CAPTURES, NUMBER OF INDIVIDUALS, AND SURVIVAL RATES OF BLUE JAYS AT THE HICKEY STUDY SITE REPORTED BY SEASON

Parameters	Spring migration (April–May)	Breeding season (June–July)	Fall migration (Aug.–Sept.)	Non-breeding season (Oct.–Mar.)
Total number of first captures	657	1144	459	113
Total number of first captures HY birds	0	805	419	18
Min–max number of Blue Jays present	7–181	11–300	6–149	2–52
Average number of Blue Jays ± SD (N)	70.2 ± 42.8^{ab} (23)	99.0 ± 71.9^{a} (24)	54.9 ± 34.8^{bc} (23)	21.3 ± 13.2^{c} (24)
Average monthly survival rates ± SD (N)	0.86 ± 0.07^{a} (23)	0.99 ± 0.04^{b} (23)	0.85 ± 0.08^{a} (23)	0.96 ± 0.03^{b} (24)

^{a,b,c} Means within a column sharing a letter are not different ($P > 0.05$).

Determination of survival rates and longevity.—Survival rates were calculated in two ways; from band returns and from sightings and recaptures of marked birds. One hundred eleven of the marked Blue Jays were reported dead. Fifty-one of the 111 band returns were from individuals initially banded within four months of fledging. Band returns from these 51 individuals were used to construct a life table (composite life table dynamic approach) and to calculate juvenile and adult survival rates (Moss et al. 1982).

In addition, seasonal and annual survival rates were calculated using the Jolly-Seber method of estimating survival rates from recapture and sighting data (Jolly 1965, Seber 1965). Survival rates calculated in this manner refer to survival on the study site. The complement of these include both mortality and emigration. Seasonal and annual survival rates were calculated for each year (1953–1976), resulting in 93 seasonal and 22 annual survival rates for Blue Jays on the Hickey study site. In order to compare mean survival rates among seasons of different lengths, monthly survival rates were extrapolated from these seasonal survival rates. Analysis of variance was used to determine whether differences in survival rates occurred among seasons, and a Tukey test ($\alpha = 0.05$) was used to determine which means were different. Regression analysis was used to test for trends in seasonal and annual survival rates between 1953 and 1976.

The longevity of 1599 Blue Jays was calculated from both recapture and sighting data. The 774 individuals that were not seen after the month in which they were banded were omitted from the analysis. For each Blue Jay, we calculated the minimum age (in years) of the bird when last observed. Because many birds were banded as adults, and many individuals were still alive after the last date of the study, these results represent minimum ages. The mean expectation of life (e_x), or average life expectancy, was calculated from the life table (Moss et al. 1982).

RESULTS

Band returns and causes of mortality.—One hundred eleven banded Blue Jays were recovered dead and reported. One hundred eight of the 111 banded Blue Jays which were reported dead were found in Madison, Wisconsin; four were recovered from other areas in Wisconsin, two were recovered in Missouri, and one in Arkansas. Three of the eight migratory individuals were banded as adults, showing that both immatures and adults may migrate.

For 68 Blue Jays (61%) the cause of mortality was unknown. Eleven (10%) were killed by cars; seven (6%) died of disease or injury; five (5%) were intentionally shot; five (5%) were killed by cats; five (5%) died by flying into windows; and 10 (9%) died from miscellaneous causes including drowning, electrocution, being caught in a trap, being caught in a fence or hanged by a string. For the 43 birds where the cause of mortality was reported, 23% were due to what might be called natural causes, 12% were directly due to humans, and 65% were an indirect result of human activities (e.g., cats, windows, cars).

Survival rates and longevity.—The annual survival rates of juvenile and adult Blue Jays as calculated from the band returns were 0.45 and 0.53, respectively (Table 3). The mean annual survival rate ± SD (N = 22) for adults and juveniles combined, calculated by the Jolly-Seber method, was

TABLE 3
COMPOSITE LIFE TABLE FOR 51 BLUE JAYS BANDED DURING HATCHING YEAR[a]

Year	Number alive at start of year (lx)	Number dying in the year (dx)	Annual mortality rate (qx)
0	51	28	0.55
1	23	14	0.61
2	9	1	0.11
3	8	3	0.37
4	5	3	0.60
>4	3	2	0.67

[a] Annual survival rates: hatching year (HY) = 0.45, after hatching year (AHY) = 0.53.

0.54 ± 0.09 (min = 0.38, max = 0.69). The mean monthly survival rates varied significantly among seasons ($F = 32.9$, $P < 0.001$) (Table 2).

Annual survival rates did not show a significant trend between 1953 and 1975 (Fig. 1). There were also no significant trends in within-season survival rates during spring migration ($r = 0.04$, df = 21, $P > 0.5$), the breeding season ($r = 0.04$, df = 21, $P > 0.5$), fall migration ($r = 0.23$, df = 21, $P > 0.05$), or the non-breeding season ($r = 0.39$, df = 22, $P > 0.05$).

The average life expectancy (e_x) for Blue Jays calculated from the life table was 1.4 years. The longevity of Blue Jays calculated from sightings and recaptures of marked birds was as follows: 1105 (69%) Blue Jays were last observed when less than two years old; 43 (3%) of the banded jays lived to be at least seven years old (Fig. 2). Two birds were last seen at a minimum age of 13 years and two jays lived at least 14 years. One of the 14-year-old Blue Jays was banded as an adult male in 1957. He was observed on the Hickey site sporadically between 1957 and 1970. In 1970, at the minimum age of 14, he was mated and feeding young.

Abundance of Blue Jays.—The numbers of Blue Jays reported on the Hickey study site during December were positively correlated with the numbers of Blue Jays reported per party hour on the Madison Christmas Bird Count during the same years (Fig. 3). This positive correlation provides support for the assumption that the number of jays reported by the Hickeys were representative of numbers within the Madison area and not merely a reflection of conditions within one backyard. As a result, fluctuations noted at this site will be interpreted as representative of changes occurring over a larger area.

The average number of Blue Jays present within a season varied significantly among seasons ($F = 11.9$, $P < 0.001$), with peak numbers

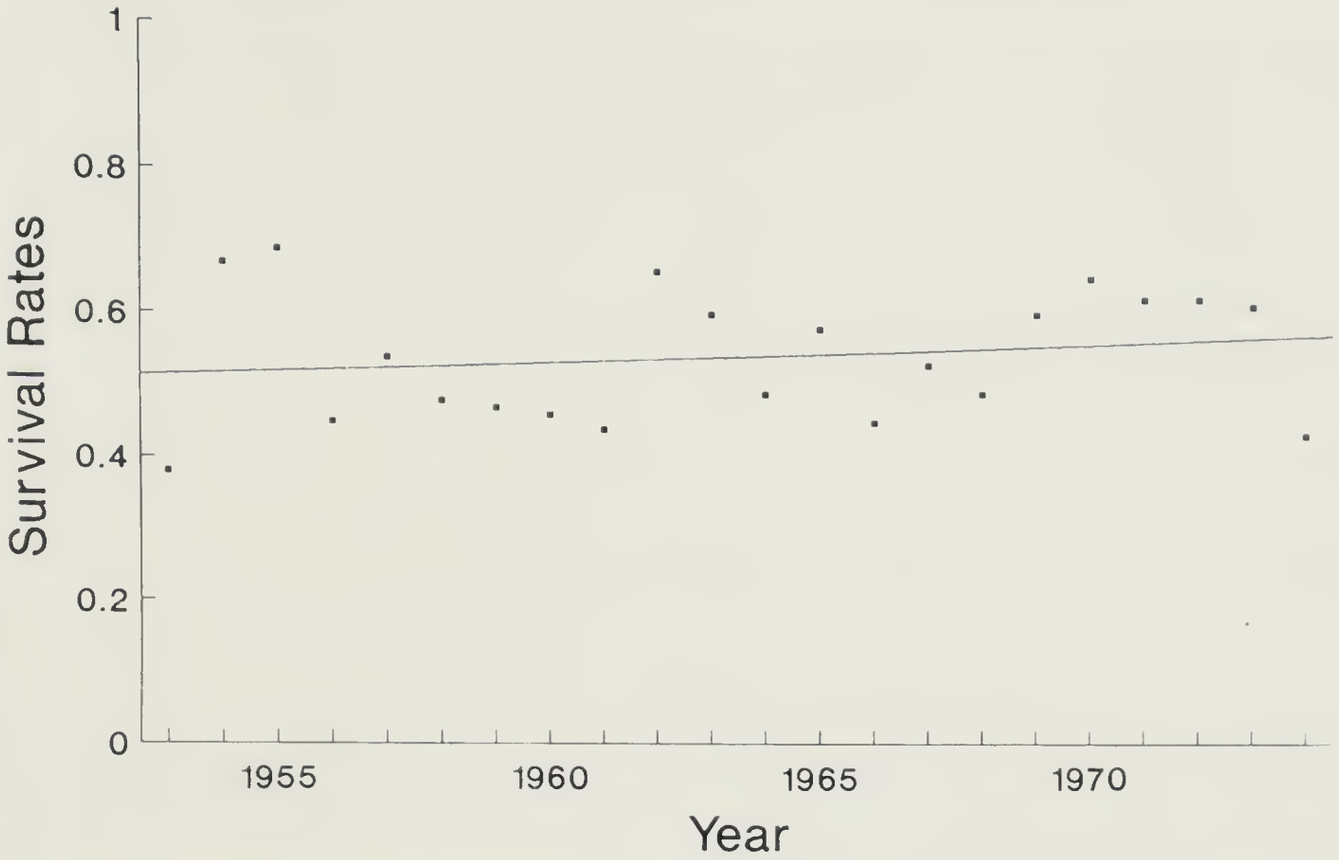

FIG. 1. Annual survival rates of Blue Jays 1953–1975 ($r = 0.18$, df = 20, $P > 0.25$).

occurring during the breeding season and low numbers occurring in the late fall and winter (Table 2).

The total number of Blue Jays present annually on the Hickey site showed a significant increasing trend between 1953 and 1975 (Fig. 4). When the years were broken down into biological seasons, the number

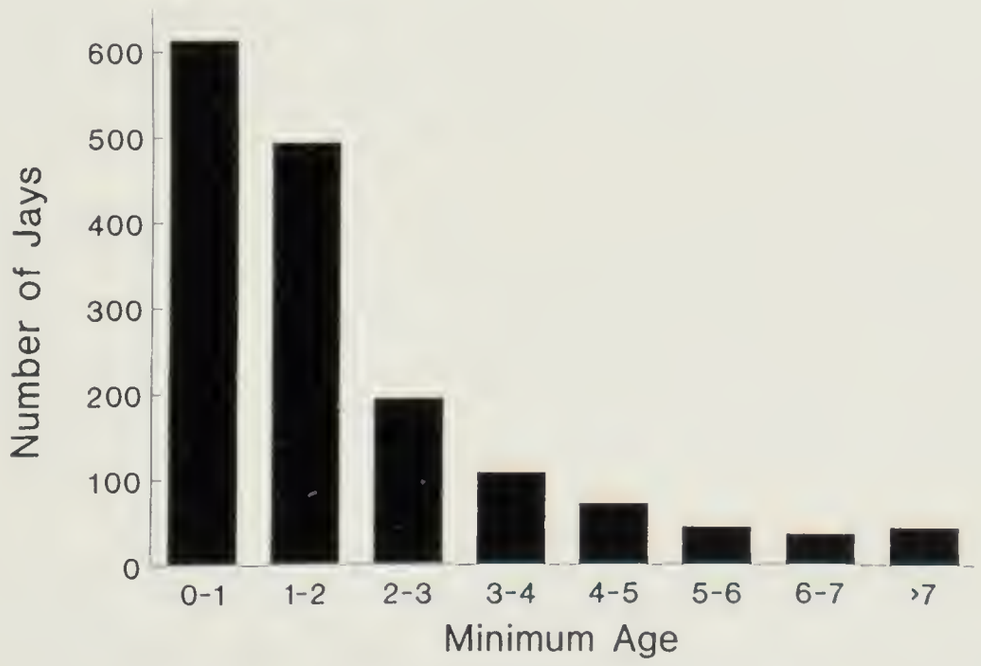

FIG. 2. Numbers of Blue Jays surviving to each age class (N = 1599).

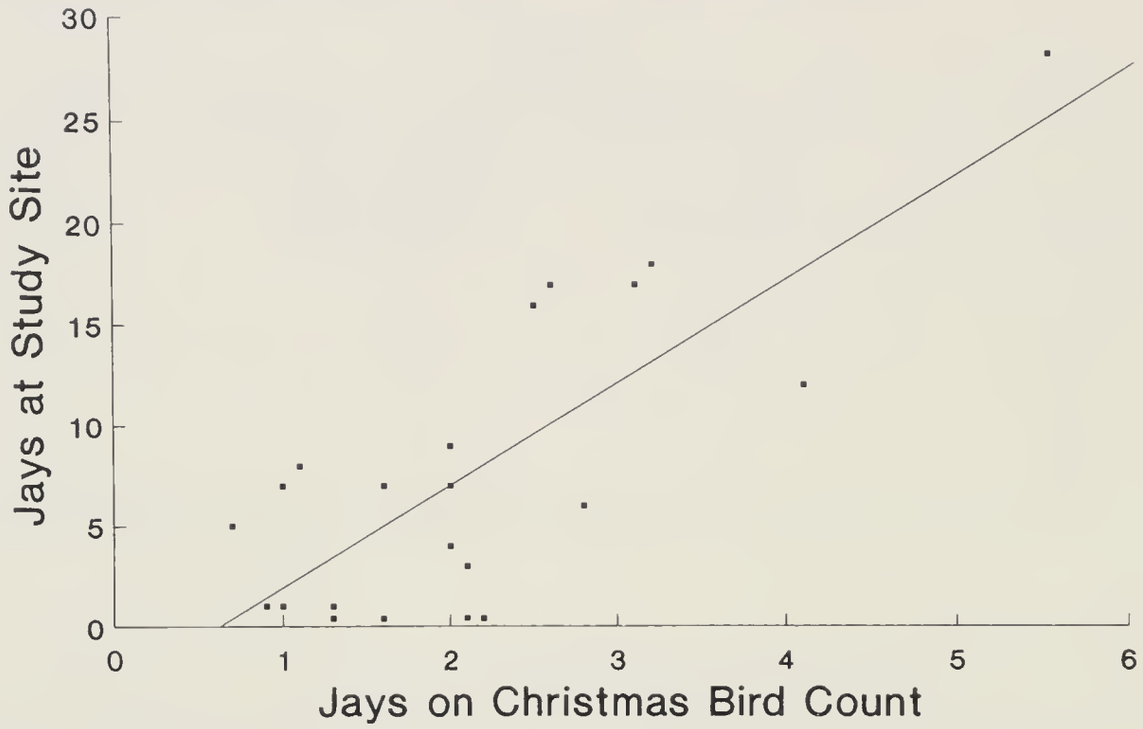

FIG. 3. Number of Blue Jays reported at the Hickey study site each December 1953–1975 and number of Blue Jays reported per party hour on annual Audubon Christmas Bird Counts in Madison, Wisconsin, 1953–1975 ($r = 0.78$, df = 20, $P < 0.001$).

of Blue Jays showed a significant increasing trend between 1953 and 1976 during spring migration ($r = 0.42$, df = 20, $P = 0.05$), the breeding season ($r = 0.57$, df = 21, $P < 0.05$), and fall migration ($r = 0.46$, df = 21, $P < 0.05$). The number of jays present during the non-breeding season showed no significant trend ($r = 0.08$, df = 22, $P > 0.5$).

Number of Blue Jays and mast abundance.—The number of Blue Jays observed during fall migration was not correlated with mast abundance ($r_s = 0.3$, N = 15, $P > 0.25$). The number of Blue Jays present on the Hickey study site during the non-breeding season increased with increasing mast abundance, but the trend was not significant ($r_s = 0.33$, N = 15, $P > 0.10$) (Fig. 5).

Age ratios.—The average ratio ± SD of juvenile to adult Blue Jays reported during the breeding season was 0.51 ± 0.35. The average ratio ± SD of juveniles to adults reported during the fall migration period was 0.53 ± 0.24. The age ratios showed no significant trends between 1953 and 1976 during either the breeding season ($r = 0.11$, df = 21, $P > 0.5$) or during the fall migration period ($r = 0.13$, df = 21, $P > 0.5$).

DISCUSSION

Survival rates, causes of mortality and longevity.—The mean annual survival rate of Blue Jays calculated in this study was similar to rates previously reported for Blue Jays and other passerines (Hickey 1952, Welty 1975, Loery and Nichols 1985). However, annual adult survival

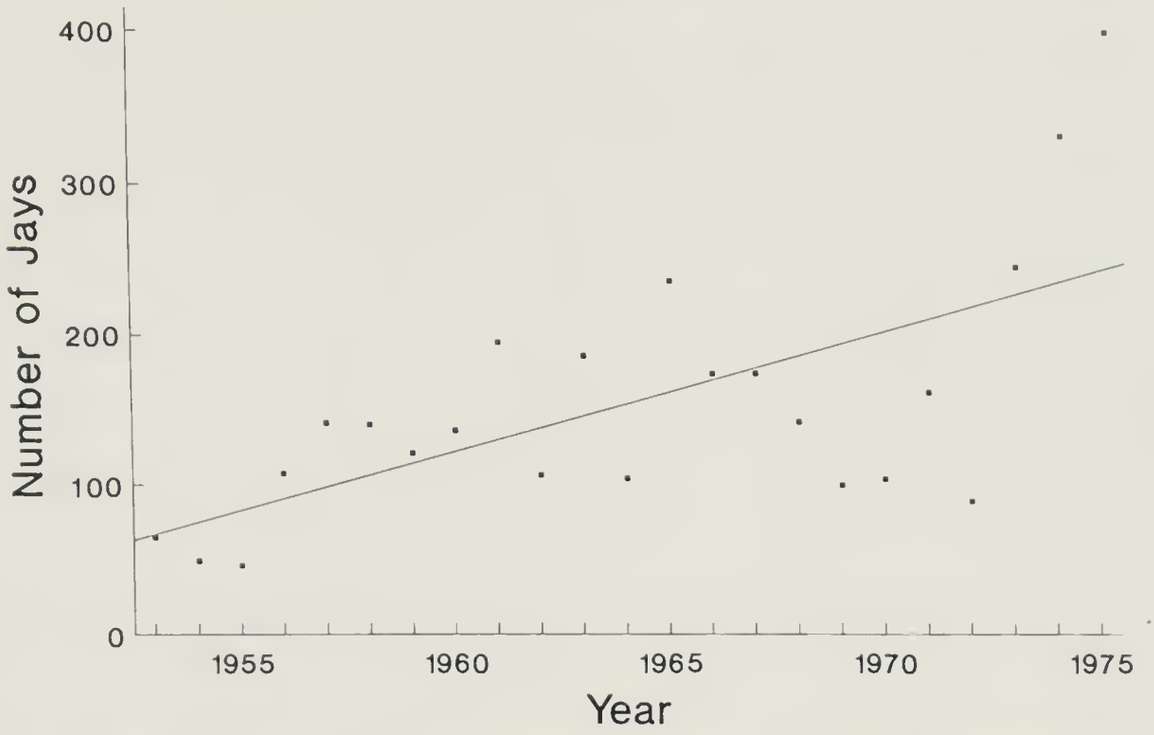

FIG. 4. Total number of Blue Jays reported annually at the Hickey study site 1953–1975 ($r = 0.53$, df = 20, $P < 0.05$).

rates were well below those reported for the cooperatively breeding Florida Scrub Jay ($\bar{x} = 0.82$) (Woolfenden and Fitzpatrick 1984). When broken down into seasons, Blue Jays had higher survival rates during the breeding and non-breeding season than during the two migratory periods, suggesting that seasonal differences in survival estimates are a result of emmigration and not higher mortality rates.

The primary causes of mortality for Blue Jays in our study were a result of human activities. However, band recoveries do not provide an unbiased sample of causes of mortality. People are much more likely to find a bird that flies into their window or is brought in by the cat than a bird killed by a hawk or dead from disease. The reported causes of mortality do, however, provide information on the hazards facing songbirds residing in suburban areas.

The oldest Blue Jays reported from five other long-term banding studies were nine years (Bryens 1949, Laskey 1958); 12 years (Harding 1944); and 13 years (Bunting 1944, Beals 1952). The longevity record as reported by the Bird Banding Laboratory is 18 years old (Clapp et al. 1983). The 14-year-old Blue Jay reported in our study is possibly the oldest known breeding Blue Jay.

Seasonal and annual fluctuations in Blue Jay numbers.—Within the year, Blue Jay numbers fluctuated seasonally corresponding with changes in the annual cycle. The lowest number of jays occurred during the winter months. Racine and Thompson (1983) reported winter group sizes varying from 14–49 individuals. The jays in their study were also associated with

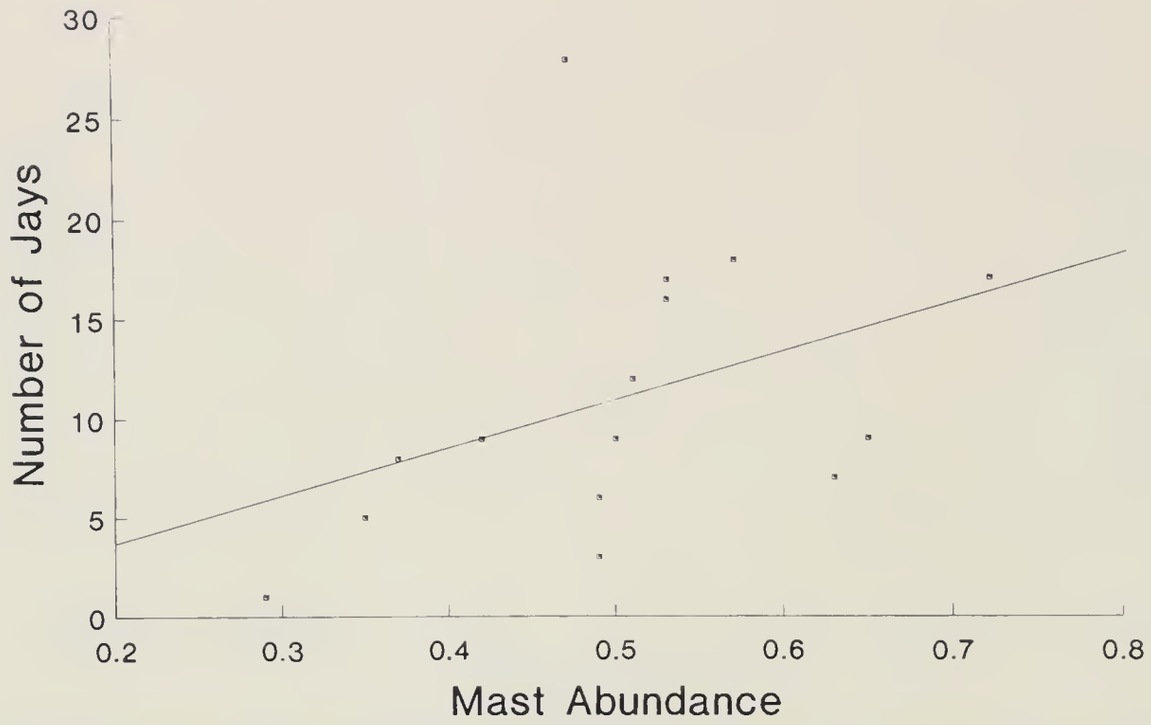

FIG. 5. Abundance of acorn mast in southern Wisconsin (1953–1969) and number of Blue Jays reported at the Hickey study site during the same years ($r_s = 0.33$, N = 15, $P > 0.10$).

a bird feeder. Winter group size in our study showed similar variation. The number of jays increased during the migratory period and peaked in the summer when young Blue Jays entered the population. Numbers declined after fall migration. The abundance of Blue Jays fluctuated among years, but numbers of wintering jays were not correlated with local mast abundance, an important food source for Blue Jays. Smith (1986) attributed variation in wintering Blue Jay numbers in the Ozarks to variation in mast abundance. However, we are not convinced that the data support this conclusion. Out of 369 comparisons made between numbers of jays and mast abundance, 341 resulted in no correlation, seven were negative correlations, and 21 were positive correlations (Smith 1986). Although other researchers have reported mass migrations of Blue Jays out of northern areas in association with low mast abundance (Broun 1941, Nunneley 1964), in our study numbers of migrating jays were not correlated with statewide mast abundance.

Even if Blue Jay numbers do fluctuate with mast abundance, the method of estimating acorn abundance used in our study may be too crude or subjective to detect trends. In addition, Blue Jays in our study were individuals that obtained seed from a bird feeder. Because feeders provide a continuous supply of food, jays which use feeders may be less dependent on acorn mast and less likely to migrate during years of poor mast abundance.

Population trends 1953–1976.—The total number of jays reported an-

nually increased significantly between 1953 and 1976. When each season was examined separately, this trend was noted in all seasons except the non-breeding season. Other researchers using Audubon Christmas Bird Count data, Breeding Bird Census data, and breeding censuses at the same sites over time, have reported increased populations of Blue Jays in both the midwest and northeastern United States during approximately the same time period (Bock and Lepthien 1976, Smith 1986, Wilcove 1988, Terborgh 1989). Increasing populations of Blue Jays have been attributed to an increase in suburban development and the amount of food available at winter bird feeders (Bock and Lepthien 1976, Terborgh 1989). It has been hypothesized that with an increased food supply from bird-feeders, Blue Jays may have higher winter survival rates or may be less likely to migrate in fall (Bock and Lepthien 1976, Terborgh 1989).

If the increased abundance of Blue Jays is a result of winter bird feeders improving winter survival rates, we predict the following: (1) bird feeders are an important source of food to wintering Blue Jays; (2) individuals with access to feeders have higher survival rates than those without access to feeders; and (3) winter survival rates of Blue Jays increased during the years of our study.

If the increased abundance of jays was a result of winter bird feeders changing migratory behavior, we would predict: (1) bird feeders are an important source of food to wintering Blue Jays; (2) the migratory behavior of Blue Jays is flexible enough to respond rapidly to changes in the local food supply; and (3) the number of migrating Blue Jays declined during the years of our study.

Since the physical and nutritional condition of birds can influence the proportion of the population that breeds and the clutch size (Murton and Westwood 1977), a third possibility is that the increase in abundance of jays is a consequence of higher reproductive rates resulting from the increase in food supply provided by bird feeders. Predictions arising from this hypothesis include: (1) bird feeders are an important source of food; (2) all adult Blue Jays do not breed in every year, or the clutch size of Blue Jays is variable; and (3) reproductive rates increased during the years of this study.

All three hypotheses proposed assume that Blue Jays are using bird feeders in the winter and that these feeders provide an important source of food. Brittingham and Temple (1989) surveyed 624 people who feed birds throughout Wisconsin and found that over 90% of them reported Blue Jays regularly visited their feeders during the winter. These results suggests that bird feeders are an important food source to wintering jays.

The survival hypothesis predicts that Blue Jays with access to feeders have higher survival rates then those without access to a supplemental

food source. In northern regions, the availability of food in winter is considered to be an important factor influencing survival rates (Lack 1954, 1966). In Wisconsin, Black-capped Chickadees (*Parus atricapillus*) with access to bird feeders have higher survival rates than individuals without access to feeders (Brittingham and Temple 1988). Bird feeders may have a similar effect on Blue Jay survival rates.

The third prediction from the survival hypothesis is that winter survival rates show an increasing trend during our study. We did not detect a change in annual or seasonal survival rates during the 23 years of this study. This does not, however, preclude changes in winter survival rates as a cause of changes in numbers of jays. Our study was conducted at a bird feeder, so any benefit from feeders would have occurred throughout the study, and any banded Blue Jays were feeder users. If bird feeders do increase winter survival rates, survival rates of jays in the Madison area would probably have increased during the years of this study, as the number of people residing in Madison and feeding birds increased. The local increase in survival rates might then result in the increased abundance of Blue Jays detected at the Hickey banding station. In addition, the positive rate of population growth exhibited by the Blue Jay population may have resulted from a change in survival rates occurring prior to the years of this study.

According to the migration hypothesis, Blue Jays have changed their migratory behavior in response to a change in food supply. The Blue Jay is a facultative migrant. During any particular year, the local Blue Jay population consists of both resident and migratory individuals. The subset of individuals that migrate and the causes of migration have been the subject of much debate (Gill 1941, Pitelka 1946, Laskey 1958, Wenger 1975). The most plausible explanation is that the majority of Blue Jays are sedentary but will migrate during years with poor food supplies (Wenger 1975). As a result of this migration strategy, changes in migratory behavior could occur rapidly if changes in the habitat or food supply favored residents over migrants.

A second prediction from the migration hypothesis is that our data show a decline in the numbers of birds banded during the spring and fall migration periods. We did not detect a decline in migrating jays. Instead, between 1953 and 1976 numbers of jays increased during both the migratory periods and remained constant during the winter.

According to the reproduction hypothesis, the increased abundance of Blue Jays resulted from an increase in reproductive rates. In Blue Jays, first year birds typically do not breed (Goodwin 1986). In this study, a few first year birds were observed breeding, but we do not have any information on the proportion of first year birds that bred. We do have

data on the proportion of juvenile to adult Blue Jays banded during each year of the study. Although caution should be used in interpreting changes in age ratios (Caughley 1974), if reproductive rates had increased significantly during the years of our study, we would expect to see an increase in the ratio of juveniles to adults banded during the breeding season and fall migration. We did not detect a change in age ratios during either time period, suggesting that a significant change in reproductive rates did not occur.

During the years of our study, the abundance of Blue Jays increased. There is no clear explanation for the observed increase in abundance. The data are most consistent with the hypothesis that regional changes in survival rates occurred either during or prior to the years of this study and that these changes were reflected in larger numbers of Blue Jays.

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EFFECTS OF PREDATOR PRESENCE ON THE NESTING DISTRIBUTION OF WHITE-CROWNED PIGEONS IN FLORIDA BAY

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Abstract.—From 1987–1989, we conducted surveys throughout Florida Bay, Card and Barnes sounds, the southern portion of mainland Florida, and the mainline keys south to Long Key to determine the breeding distribution of White-crowned Pigeons (*Columba leucocephala*). We found pigeons nesting on 88 of 169 keys over a wide range in Florida Bay, Card and Barnes sounds, and in one location on the mainline Keys. Their nesting distribution appeared to be limited by the presence of raccoons (*Procyon lotor*). Of the 33 keys on which we found evidence of raccoons, only six had nesting White-crowned Pigeons. Other potential nest predators did not seem to influence nesting distribution. In Florida, White-crowned Pigeon breeding populations apparently are limited by the availability of nesting sites without raccoons. *Received 16 Nov. 1990, accepted 8 March 1991.*

The breeding distribution of the White-crowned Pigeon (*Columba leucocephala*) includes the Bahama Islands, the Greater Antilles, the Lesser Antilles south to Antigua, and the Florida Keys from the Marquesas Keys north to Elliott Key (Bent 1932, Goodwin 1967, AOU 1983). Additional breeding populations occur on offshore islands on the Caribbean coasts of Mexico (Quintana Roo), Belize, Honduras, Nicaragua, and possibly Panama (Bent 1932, Wetmore 1968, AOU 1983). The non-breeding range is slightly larger and includes peninsular Florida north to Fort Pierce, the Lesser Antilles south to St. Lucia and western Panama (AOU 1983). Habitat destruction, the taking of squabs, and over-harvesting of adults caused several authors to express concerns over decreasing population levels (Wetmore and Swales 1931, Owre 1978, Wiley 1979, Norton and Seaman 1985). Arendt et al. (1979) reviewed the status of the White-crowned Pigeon and listed populations as decreasing in the Bahama Islands, Cuba, Haiti, Dominican Republic, Puerto Rico, the U.S. and British Virgin Islands, Anguilla, St. Martin, and Nicaragua. Increasing or stable populations were cited in Florida, the Cayman Islands, Jamaica, Barbuda, Antigua, Mexico, Belize, Honduras, and Panama (Arendt et al. 1979).

The White-crowned Pigeon is listed as threatened in the state of Florida (Owre 1978). In 1976, the breeding population in south Florida was estimated to be 5000 pairs (Reeves 1977). However, the present population is mobile and widely dispersed even in the breeding season making

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it difficult to obtain repeatable population estimates. Current protection has allowed the population to increase, but rapid clearing and development of tropical hardwood forests in south Florida is still a concern (Ogden 1973, Owre 1978).

White-crowned Pigeons are known to nest on offshore mangrove islands (Howell 1932), but little information is available on their nesting distribution. The objectives of the present study were to define the White-crowned Pigeon's breeding distribution in Florida Bay and investigate the factors limiting this distribution. Allen (1942) reported that raccoon (*Procyon lotor*) colonization of a mangrove island in Florida Bay supporting nesting Roseate Spoonbills (*Ajaia ajaja*) caused abandonment of the nesting site. We investigated the possibility that predators may have a similar influence on the nesting range of White-crowned Pigeons in Florida Bay.

METHODS

Study area.—We surveyed breeding White-crowned Pigeons on all mangrove keys throughout an area of approximately 1850 km^2 including Florida Bay, Barnes and Card sounds, the southern coast of the mainland, and the mainline Keys from Elliott Key south to Long Key (Fig. 1). An additional survey was conducted over a 63-km^2 portion of Whitewater Bay (Fig. 1) in mainland Everglades National Park. Most of the study area is within Everglades National Park, and the nesting islands are legally protected from human disturbance.

Florida Bay is a large, shallow estuary. The eastern bay is characterized by relatively deep (1–2 m) basins divided by narrow (often <200 m), shallow (<30 cm) banks (Schomer and Drew 1982, Powell 1987). Many of the keys within the eastern bay are situated along these banks (Fig. 1). Areas of higher elevations on the banks support red mangroves (*Rhizophora mangle*) which over time may develop into keys. In the western bay, the banks are larger, with maximum widths of more than 10 km. The keys in Florida Bay are typically fringed with dense stands of red and black (*Avicennia germinans*) mangroves. The outer edge is typically the highest part of the key and grades into a sparsely vegetated and shallowly flooded central lagoon. Some keys in the western portion of Florida Bay show the opposite configuration; a mangrove fringe grading into a higher elevation scrub forest.

The southern coast of the mainland and the mainline Keys are also bordered by red mangrove. Interior to the mangrove zone is a transitional zone of black mangrove, buttonwood (*Conocarpus erectus*) and salt-tolerant herbaceous plants. On the mainline Keys, the higher elevations support tropical hardwood forests. South of central Key Largo, much of this habitat has been cleared for development. On the mainland, the transitional zone grades to extensive mangrove forests interspersed with grass-dominated marshes, low elevation hardwood forests, and open water.

Surveys.—We conducted surveys for White-crowned Pigeons from early July through late August, typically the period of peak nesting activity (Bancroft and Bowman, unpubl. data). Most of the surveys were in 1987–1989; a few initial surveys were done in 1986. Surveys were conducted from sunrise to approximately 13:00 h. We followed the methods in Florida's Breeding Bird Atlas Handbook (Noss et al. 1985) to determine nesting status for each area searched. We walked through all suitable habitat when searching small keys; for larger keys, we set a pre-determined search time (generally 30–50 min) and covered as much of the key as possible during that period. For each area searched, we recorded the status and number

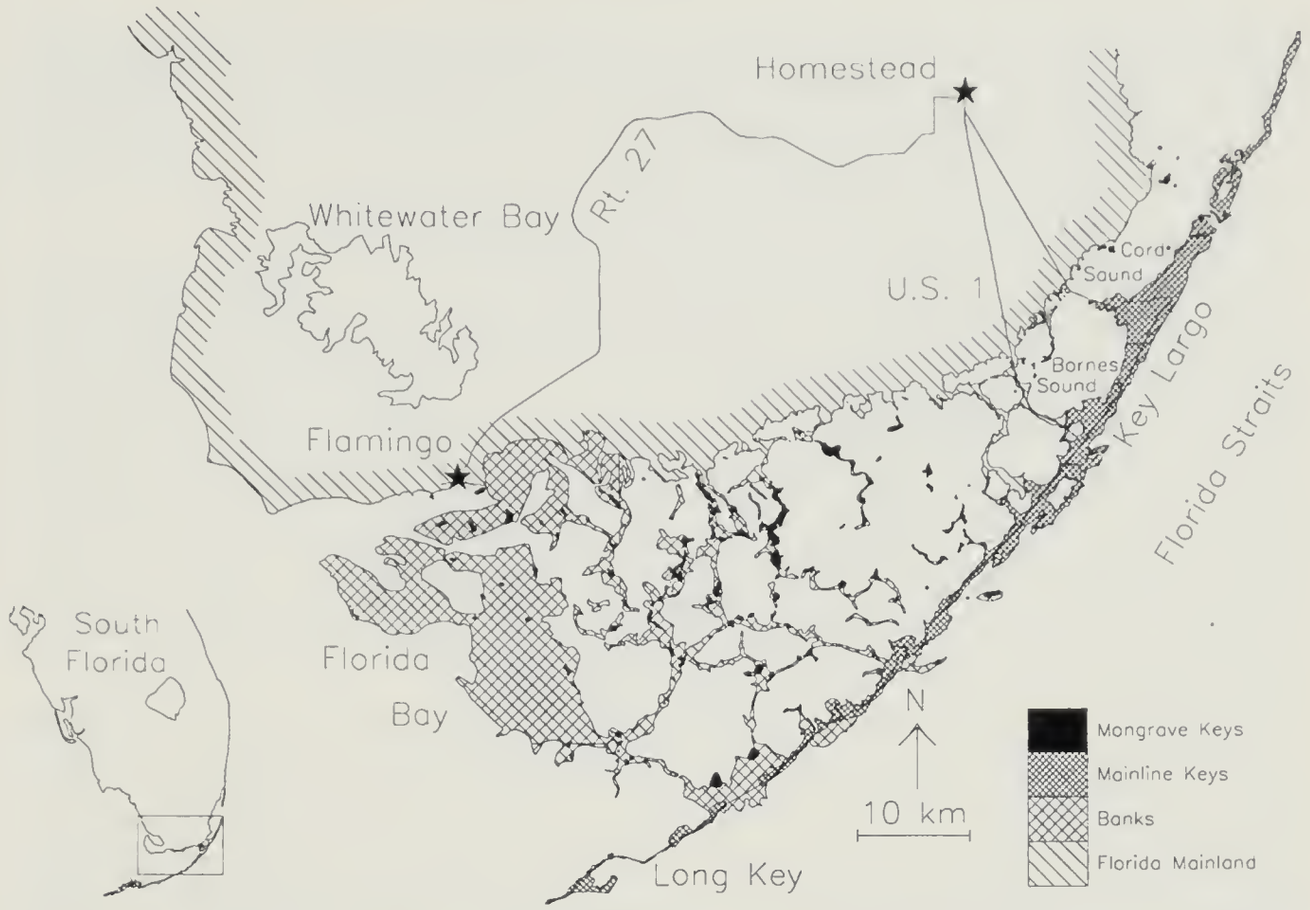

FIG. 1. Southern Florida study area and the arrangement of banks and mangrove keys within Florida Bay.

of active nests, number of old nests, and collective search time. In addition to recording White-crowned Pigeon nests, we noted the presence or sign of all potential nest predators. We determined nest detection rate by adding the number of old and new nests found in the area and dividing by the total time spent searching the area. A frequency distribution of nest detection rates revealed a natural break at 0.08 nests/min. We used this value to distinguish between areas of high (>0.08 nests/min) and low (≤0.08 nests/min) nest detection rates.

RESULTS

White-crowned Pigeon nesting distribution.—We searched 169 mangrove keys in Florida Bay, Card Sound, and Barnes Sound. A total of 384 nests were found in 204.1 h of surveys (number of nests found on individual keys, presence of predators, and survey times are available from the authors upon request). Number of nests found per key ranged from one on many keys to 22 on West Key. We found no nests on the mainland or in Whitewater Bay in 23.7 h of censuses. One nest was observed in 1990 in a development at the north end of Key Largo. No additional nests were found in 11.0 h of surveys on the mainline Keys from northern Key Largo north to Elliott Key. Development in this area is sparse and a substantial percentage of land is within Biscayne National Park, Crocodile Lake National Wildlife Refuge, or Key Largo Hammocks State

Botanical Site. National Audubon Society personnel have conducted extensive field work, including breeding bird surveys, in the tropical hardwood forests from north Key Largo to Long Key and have not detected any additional nesting activity. Therefore, we are confident that nesting on the mainline Keys is rare.

White-crowned Pigeon nests were found on 88 of the 169 mangrove keys surveyed (52%). Keys with nesting pigeons were widely distributed across Florida Bay (Fig. 2). Over an east–west gradient, White-crowned Pigeon nesting keys spanned the entire bay with the exception of two keys in the extreme western bay. Except for nesting in three disjunct areas, the main nesting distribution in the central bay was much farther from the mainland than in either the extreme eastern or western portions. In general, keys closest to the mainland did not support nesting pigeons, whereas keys closest to the mainline Keys often did.

Nest detection rates ranged from 0.01 to 0.71 nests/min. Because the keys vary substantially in size, similar nest detection rates do not allow direct comparisons of absolute population sizes. The area of highest nest detection rates was in the central portion of the bay, with the distribution constricted away from both the mainland and the mainline Keys (Fig. 2). Although several outlying keys did have high nest detection rates, detection rates in the extremities of the range usually were lower.

Two keys on the Florida Straits side of the mainline Keys had small numbers of nesting White-crowned Pigeons (Fig. 2). Also, two keys in Card Sound supported nesting White-crowned Pigeons (Fig. 3). The nesting location in Barnes Sound was the closest (0.3 km) to the mainland that we encountered. White-crowned Pigeons were nesting in isolated clumps of red mangroves on a spoil bank adjacent to Card Sound Road, separated from the mainland by a canal.

Distribution of nest predators.—Both avian and mammalian nest predators were recorded during our surveys. Potential avian nest predators were Red-winged Blackbirds (*Agelaius phoeniceus*), Laughing Gulls (*Larus atricilla*), and American Crows (*Corvus brachyrhynchos*). Red-winged Blackbirds were abundant throughout Florida Bay, where they occurred on 100 of 169 keys surveyed. Although Laughing Gulls were common and could be seen from the periphery of most keys, we found only three small nesting colonies during our surveys. We recorded American Crows on three keys in Florida Bay. They are common on the mainland, but are rarely observed on the mainline Keys.

We recorded the presence of four potential mammalian predators during the nesting surveys. Few were seen; most were identified by tracks or scat. The Virginia opossum (*Didelphis virginiana*) and bobcat (*Lynx rufus*) were found only on the mainland, the mainline Keys, and one key each

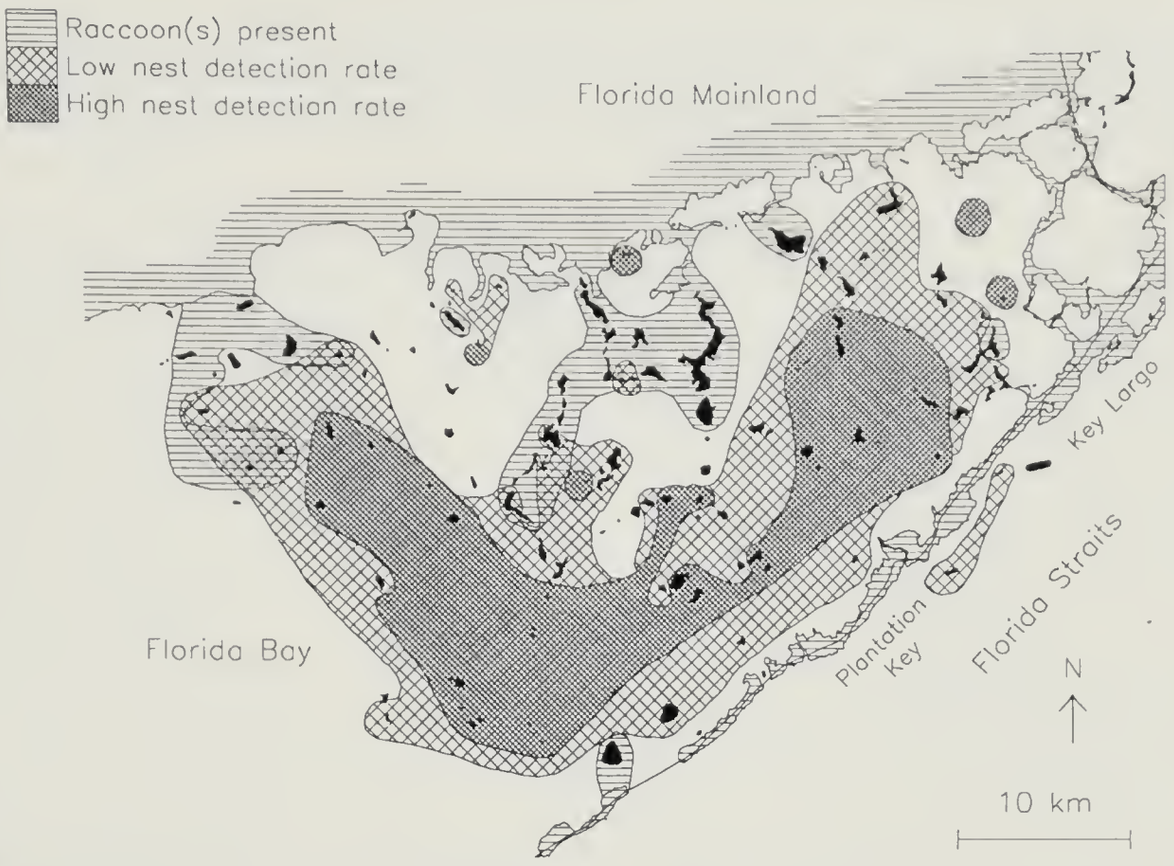

FIG. 2. Distribution of raccoons and areas of high and low nest detection rates of White-crowned Pigeons in Florida Bay, 1987–1989. Mangrove keys are shaded in black.

within Florida Bay. We recorded rats (*Rattus rattus* and *Rattus* sp.) on eight keys, widely dispersed throughout Florida Bay. Several keys harboring rats were not directly connected to the mainland or the mainline Keys by banks.

Raccoons were present and often common on the mainland and mainline Keys. In Florida Bay, and Card and Barnes sounds, we found evidence of raccoons on 33 keys (Figs. 2 and 3). The most widespread populations occurred in the north central and northwestern portions of the bay. In the northwestern bay, raccoons were found on seven keys. These keys, although widely separated, are connected by extensive banks (Fig. 1) that are exposed at low tides. In the north central bay, raccoons were located on 21 keys. All keys in this area are connected to each other and the mainland by banks (Fig. 1). In Figure 2, we depict the distribution as being continuous throughout this area. However, evidence of raccoon presence was found on only 21 of 32 (including the southernmost) keys within this chain. We feel raccoons must at least use the remaining keys in this range as travel lanes and are present on all of them for some portion of the year. Two keys adjacent to the mainline Keys had raccoon populations (Fig. 2).

Degree of overlap between potential nest predators and nesting locations.—Red-winged Blackbirds had the highest proportion of overlap with

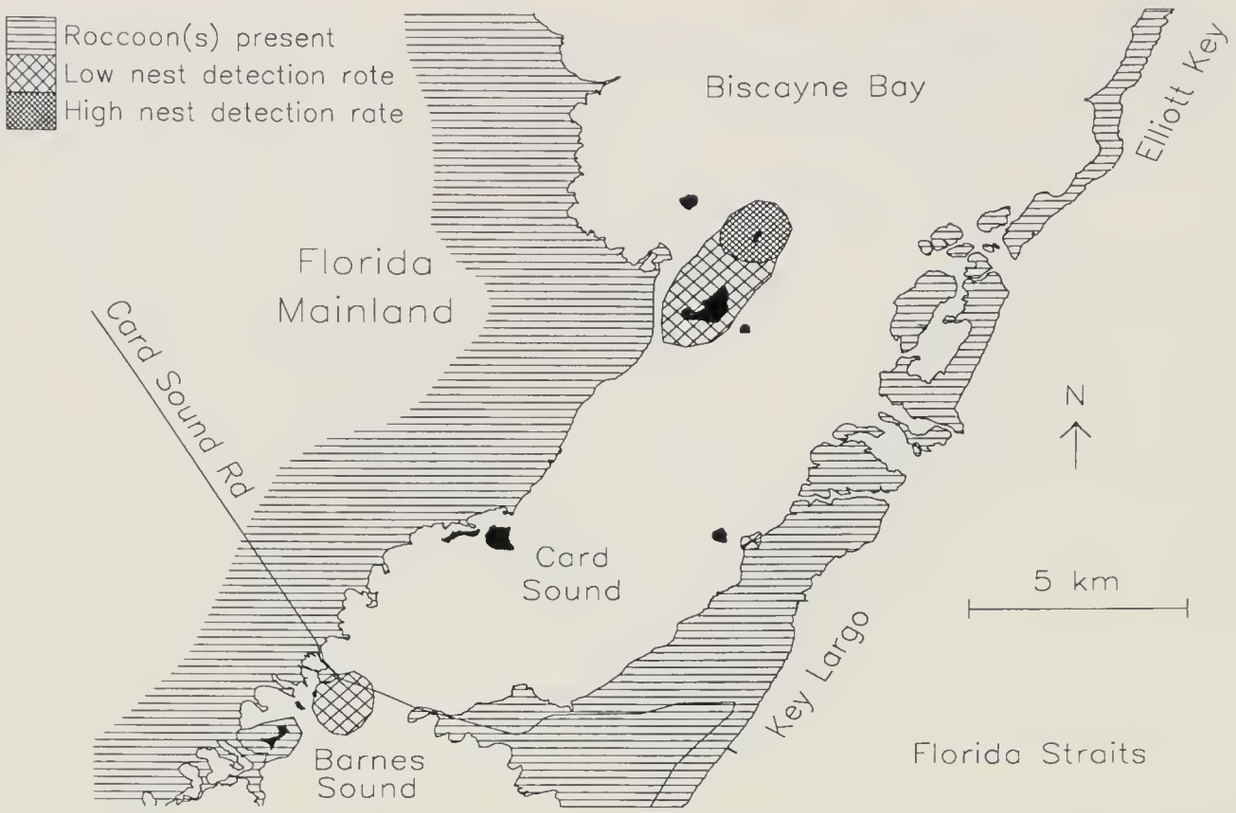

FIG. 3. Distribution of raccoons and areas of high and low nest detection rates of White-crowned Pigeons in Card and Barnes sounds, south Florida, 1987–1989. Mangrove keys are shaded in black.

nesting White-crowned Pigeons. They occurred on 59 of 88 (67%) keys with nesting pigeons. This occurrence rate was actually higher than we found on non-nesting keys ($G = 4.43$, $P < 0.05$).

The three keys on which we recorded nesting Laughing Gulls all had nesting White-crowned Pigeons. We were mobbed by Laughing Gulls on an additional seven keys, all of which supported nesting White-crowned Pigeons. Two of the three keys on which we recorded American Crows had nesting White-crowned Pigeons. All three of the keys with crows also had wading bird or Brown Pelican (*Pelecanus occidentalis*) and Double-crested Cormorant (*Phalacrocorax auritus*) colonies.

Of the eight keys that supported rats, five had nesting White-crowned Pigeons. Three of these keys had high pigeon nest detection rates. Neither of the keys on which opossums or bobcats occurred had nesting pigeons. Of the 33 keys that supported raccoons, only six (18%) had nesting White-crowned Pigeons. The proportion is similar (9 of 44 keys, 20%) if the entire chain of keys in the north central bay is considered to be occupied by raccoons. All of the keys that supported both raccoons and pigeons had low nest detection rates (range = 0.01 to 0.08 nests/min).

The proportion of nesting keys with raccoons is significantly different than the proportion of non-nesting keys with raccoons ($G = 19.97$, $P < 0.005$). The maximum number of nests found on keys containing raccoons

was seven. Three keys had four to seven nests; however, these were small keys and the total number of nests found probably represents most of the nesting population.

DISCUSSION

White-crowned Pigeon nests are relatively easy to locate. Adults remain on nests until an intruder approaches closely and then they flush with loud wing claps. Thus, we feel that we have described accurately the current nesting distribution of White-crowned Pigeons in Florida Bay and Card and Barnes sounds. White-crowned Pigeons also nest south of Long Key on offshore islands along the mainline Keys, but the current nesting distribution and population status in this area is unknown (T. Wilmers, pers. comm.).

Although Figures 2 and 3 represent the current breeding distribution of White-crowned Pigeons, temporal shifts in distribution may occur even in areas with high nest detection rates. West Butternut, a small key on which we monitored reproductive success, experienced a reduction in nesting pigeons from 1987–1989 (with 68 nests in 1987, 15 nests in 1988, and only one nest in 1989), whereas Middle Butternut, located 0.5 km away, supported more than 100 nests throughout this period (Bancroft and Bowman, unpubl. data). We have no explanation for this decrease.

In Florida Bay, pigeon nesting occurs in a broad, V-shaped band that diverges from the mainland in the central portion of the bay. Low nest detection rates or the absence of pigeons on keys with a high incidence of raccoons suggests that raccoons at least limit the distribution of high density nesting areas. The distribution of raccoons is nearly parapatric with that of pigeons. The only overlap occurred at the outer edges of the nesting range on six keys with low nest detection rates. Four of these keys had nest detection rates less than 0.04 nests/min, and two keys had only one old nest. We found no evidence of nesting by White-crowned Pigeons on the mainland or most of the mainline Keys. We feel that this is a response to high densities of mammalian predators. Wiley (1979), however, reported six nesting locations on Puerto Rico, suggesting that in other localities, mammalian predators may not exert such an influence.

The presence of sympatric raccoons and nesting pigeons may indicate recent raccoon colonization of a particular key. We have no indication of how effective raccoons are as predators on White-crowned Pigeon nests. They have been cited as nest predators on a variety of both ground- and tree-nesting species (Allen 1942, Lopinot 1951, Rearden 1951, Kilham 1986, Frederick and Collopy 1989, Post 1990). Wilcove (1985) felt that nest predation by mammals was less significant at nests greater than 1 m above ground level. Because White-crowned Pigeons frequently nest 1–2

m above ground, colonization of a nesting key by raccoons may not immediately eliminate the pigeon population. Raccoon scats found in Florida Bay contained primarily fish, crab, and shellfish fragments. Consequently, the two species may temporarily coexist on a key.

The current raccoon distribution reflects the unique arrangement of shallow mud banks in Florida Bay. Over the past 50 years, raccoons have been observed on additional keys within Florida Bay (Allen 1942; R. Paul, W. Robertson, pers. comm.), indicating that populations may be fairly mobile. Most raccoons probably reached mangrove keys from the mainland by following these banks and swimming across deeper channels. Raccoons on the keys in the southern and eastern portions of the bay most likely colonized from the mainline Keys. Although the intracoastal waterway separates the mainline Keys from keys within Florida Bay, mud banks still allow access to these keys with minimal swimming.

Allen (1942) felt raccoon distribution and abundance in Florida Bay was correlated with the occurrence of hurricanes. Moderate to large hurricanes occur in Florida Bay at approximately 20–25 year intervals (Gentry 1974). These events most certainly decimate the raccoon population on many keys in the bay and may periodically push the raccoon range back to the mainland, allowing the central bay to remain raccoon-free.

The influence of other potential predators seems to be minimal. Red-winged Blackbirds can be effective nest predators at unattended nests (Blankinship 1977, Sprunt 1977, Bancroft and Bowman, unpubl. data). In Florida Bay, the absence of human disturbance on nesting keys probably increases nest attentiveness and diminishes the effect of blackbird predation. However, blackbird predation may be a factor in areas where human disturbance is unregulated, such as keys in the Florida Straits and in Card and Barnes sounds. The high degree of overlap between Red-winged Blackbirds and pigeons suggests that blackbirds may also avoid keys with raccoons.

All 10 keys on which we recorded Laughing Gull nesting or mobbing activity supported nesting pigeons. Frohring and Kushlan (1986) listed Laughing Gull nesting colonies on 26 keys in Florida Bay. We found White-crowned Pigeons nesting on 24 of those keys and two additional keys that were not documented as nesting sites for gulls. Therefore, we do not suspect that gulls play a major role in limiting pigeon nesting distribution. Crows (*Corvus* spp.) have been cited as nest predators in a number of other studies (Burger and Hahn 1977, Verbeek 1982, Shields and Parnell 1986). However, in Florida Bay, crow distribution seems to coincide with wading bird, pelican, and cormorant colonies. White-crowned Pigeons did not nest on two keys with major wading bird colonies in

Florida Bay, but were found in high densities in a wading bird colony in the northeastern bay. Of the three keys on which we recorded crows, one had high pigeon nest detection rates, one had a single nest, and the other had no nesting. Therefore, the influence of crows is difficult to evaluate.

We found evidence of rats on eight keys, including keys with both high and low pigeon nest detection rates. Although rats have been cited in the reduction or elimination of several ground or burrow-nesting island birds (Austin 1948, Kepler 1967, Berger 1972:86, Cruz and Cruz 1987), their presence on keys does not seem to preclude nesting by White-crowned Pigeons. Wiley and Wiley (1979) reported *Rattus rattus* depredation on White-crowned Pigeon nests in Puerto Rico when lowered water levels permitted easier access to nest trees. Given the wide (but patchy) distribution of rats and their secretive and nocturnal behavior, they may be more common than we observed during the nesting surveys. As with raccoons, rat populations may be regulated by hurricanes.

The future breeding status of White-crowned Pigeons in the Florida Keys is threatened by two factors. First, expansion of raccoons to more keys in Florida Bay could make additional islands unsuitable for nesting. Human habitation, especially in the mainline Keys has caused localized increases in raccoon populations and thus increased the probability of raccoon dispersal into Florida Bay. Second, and possibly more important to the long-term survival of the White-crowned Pigeon in south Florida, is the clearing of tropical forests. White-crowned Pigeons feed exclusively on fruits of tropical hardwood trees found in these forests and current development presents a threat to their food base. Data from this study can be used to evaluate future changes in White-crowned Pigeon demographics and may be used as an indicator of changes in the food base or predation pressure in certain parts of their nesting range. The presence of Everglades National Park has probably ensured the survival of White-crowned Pigeons in south Florida by protecting both foraging and nesting habitats. However, conservation of the remaining tropical forests on the mainline Keys may be the overriding factor that determines the future success of White-crowned Pigeons in south Florida.

ACKNOWLEDGMENTS

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Wilson Bull., 103(3), 1991, pp. 426–434

THE BODY RUFFLING DISPLAY OF THE BLACK-CAPPED CHICKADEE

VICTORIA D. PIASKOWSKI,[1] CHARLES M. WEISE,[1] AND MILLICENT SIGLER FICKEN[1,2]

ABSTRACT.—Body ruffling displays of Black-capped Chickadees (*Parus atricapillus*) consist of extreme ruffling of the breast and back feathers and often are associated with wing extension and spread primaries. Body ruffling was observed throughout the non-breeding season but was more frequent in the fall. Birds of all ages and sexes exhibited the display, but juvenile males did so most frequently. Body ruffling was directed toward individuals of any age or sex and to familiar as well as to new birds in the area. Contrary to our prediction, the display was given less frequently, rather than more frequently, toward the eventual mate of the displayer. The seasonal frequency of the display paralleled the frequency of arrival of new birds at the feeders rather than the frequency of all aggressive behavior. The display appears to function in maintaining individual distance and gaining access to food, and it is not involved in pair formation as has been suggested for other parids. *Received 21 Aug. 1990, accepted 7 March 1991.*

A key task in examining animal interactions is assessing the functions of displays (Tinbergen 1963). Responses to the displayer can reveal function in some cases, while in others the function is not immediately obvious. A type of display reported in many parids consists of extreme ruffling of the breast and back feathers, accompanied sometimes by partial wing extension (Fig. 1). The display has been ascribed a pairbonding or courtship function in the Black-capped Chickadee (*Parus atricapillus*) (Allen 1929, Ficken et al. 1985), Great Tit (*P. major*) (Hinde 1952), Willow Tit (*P. montanus*), and Marsh Tit (*P. palustris*) (Fitter 1973). In the Carolina Chickadee (*P. carolinensis*), a body ruffling posture was observed in what were apparently agonistic interactions between two or more birds, but the posture was not studied in detail (Smith 1972). Body ruffling has also been noted in autumn in Boreal Chickadees (*P. hudsonicus*) and Mountain Chickadees (*P. gambeli*) (Ficken, pers. obs.). Thus, the display is widespread in the genus but has not been analyzed in detail in any species.

We analyzed interactions involving this display in an attempt to determine its function. Two hypotheses were tested: (1) body ruffling is involved in pair formation in juveniles (i.e., first-year birds) and/or adults, and (2) it is associated with aggressive behavior among flock members,

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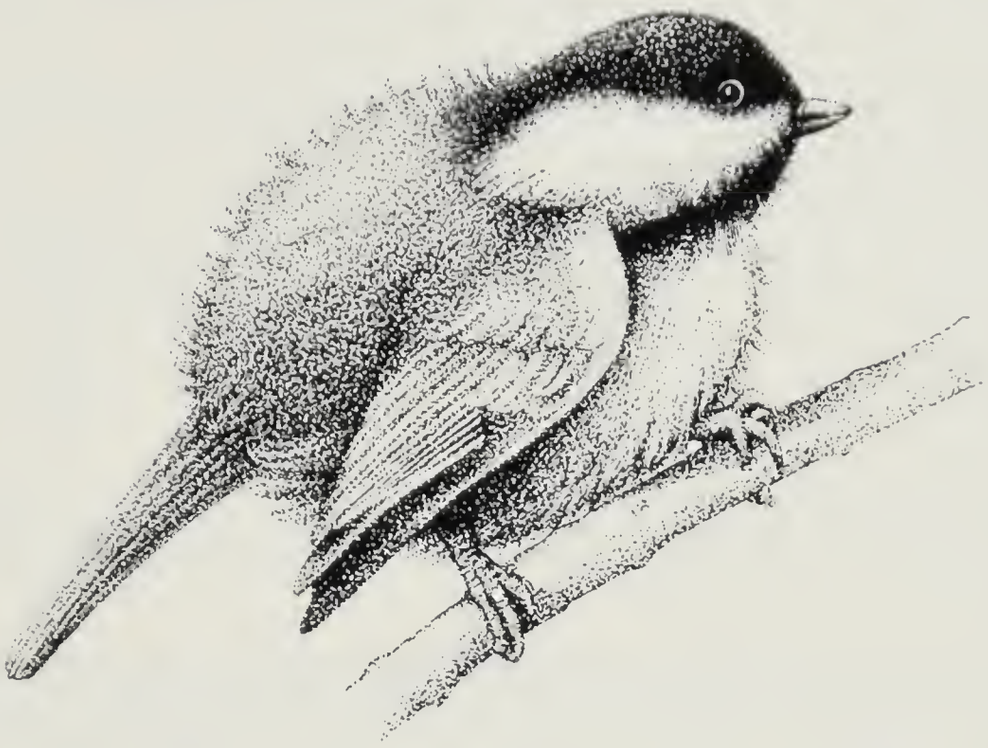


FIG. 1. Black-capped Chickadee exhibiting the body ruffling display.

especially as new birds become integrated into the flock. By studying the occurrence of the behavior for a full year, we were able to obtain data on seasonal patterns as well as on the context of usage of the display. Chickadees live in flocks of both sexes and mixed ages during the non-breeding season (Odum 1942, Glase 1973, Weise and Meyer 1979) and as monogamous pairs on territories during the breeding season (late April–July in Wisconsin).

METHODS

Since 1967, most chickadees at the Univ. of Wisconsin–Milwaukee Field Station, Ozaukee County, Wisconsin, have been color-banded for individual recognition in conjunction with studies of population ecology, vocalizations, and social behavior (e.g., Weise and Meyer 1979, Ficken et al. 1981). The birds we studied had winter flock ranges and breeding territories in a 45-ha tract of maple-beech upland forest and adjoining small patches of wetland deciduous forest. Adult chickadees were color banded by Weise in the winter and spring of 1987. Post-dispersal juveniles were captured either in special mist nets in July and early August 1987, or in the feeder traps mentioned below. Most of the observations were made at three feeders located along one edge of the forest and provisioned with waxworms (*Galleria mellonella* larvae), water and sunflower seeds (July–October), or sunflower seeds and suet (November–April). The use of three feeders enhanced observer discrimination of flocks and movements. Additional observations of territorial and courtship behavior were made in the woods at the time of territory establishment (March–April) and nesting (May–July).

The primary observer (Piaskowski) watched birds at the feeders or in the near vicinity three times weekly, mainly in the mornings. On each day, there were two sessions at each feeder at least one hour apart. In addition to description of the ruffling display, the following

TABLE 1
AGE AND SEX OF DISPLAYER AND RECIPIENT OF BODY RUFFLING DISPLAYS

	Recipient					
	Juvenile male	Juvenile female	Adult male	Adult female	Total displays given	Total bird-days
Juvenile male	30	22	15	18	85	1095
Juvenile female	11	6	4	7	28	860
Adult male	11	5	1	3	20	603
Adult female	5	0	4	1	10	653
Total displays received	57	33	24	29	143[a]	3211

[a] An additional 58 displays were observed in which one or both participants were unidentified.

were recorded: individuals visiting the feeder, times of flock arrival or departure, aggressive interactions including identity of winner and loser, kinds of vocalizations, and distances between birds when displays occurred. Notes were spoken into a tape recorder. One session, on 12 September 1987, was videotaped. Total time at the feeders for the primary observer was 220 h.

This was a blind study, i.e., the primary observer did not know the age, sex, or history of any of the birds until the study ended. New, unbanded birds were marked, aged, and sexed by Weise. Age was determined by rectrix shape (Laaksonen and Lehikoinen 1976) or skull ossification. Sex was provisionally determined by wing chord (70% of the birds) and later verified by sex-specific behavior during the breeding season (Weise 1979).

Statistical tests included the G (log likelihood ratio) test and Spearman rank correlation, r_s (Sokal and Rohlf 1981). To standardize for encounter possibilities, we used "bird-days." Each day that a particular individual was observed at a feeder was defined as one bird-day for that individual. By using dates and feeder locations, we could then estimate the number of opportunities for interaction between that bird and any other. If all displays were distributed evenly, a bird would be expected to display in proportion to the number of days it spent at the feeders. For Tables 1 and 2, the expected frequencies were calculated as follows: Table 1—expected displays = (total displays for all ages and sexes) × (number of bird-days for specific age and sex category/total bird-days for all categories). Table 2—expected displays for bird A = (bird-days for A when its mate was present/bird-days A spent with mate and non-mates) × total displays for A.

Because some individuals were observed to display more than once, our counts of displays were not truly independent. To ensure that our conclusions regarding more frequent use of the display by a particular age and sex class were not due to one or a few individuals displaying a large number of times, we prepared a standardized frequency distribution of displays for all of the 92 birds in the study. This was calculated as follows. Expected displays for each individual = total number of displays for all individuals/total bird-days for all individuals × total bird days for the individual. To obtain the frequency distribution seen in Fig. 2, we standardized for the amount of observation time on each individual as follows: (observed displays for individual − expected displays for individual)/(bird-days for individual).

RESULTS

In 64% of the 201 displays observed, wing extension with primaries spread also occurred. The display, lasting 1–2 sec, was observed on feeder

TABLE 2
BODY RUFFLING DISPLAYS DIRECTED TOWARD EVENTUAL MATE AND OTHERS[a]

	Displays to mate	Exposure to mate (bird-days)	Displays to non-mate	Exposure to non-mates (bird-days)
Juvenile male	4	368	63	3018
Juvenile female	0	260	26	2036
Adult male	0	222	19	2050
Adult female	1	104	6	933
Total	5	954	114	8037

[a] Includes only those birds whose 1988 mate is known.

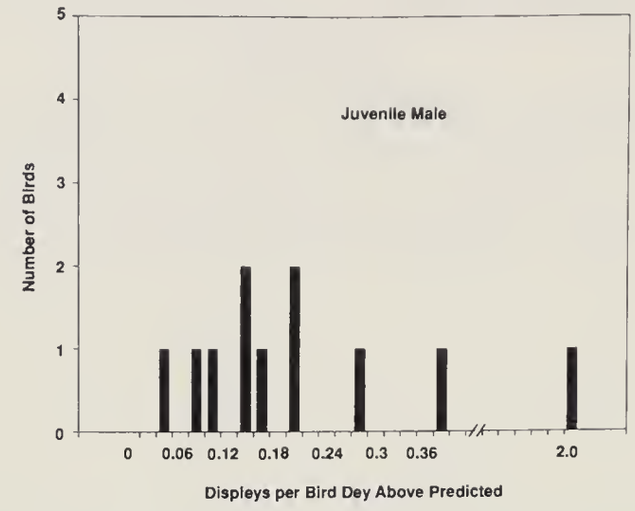
perches as well as in trees near the feeders. Body ruffling was given only in close range encounters, when inter-individual distance was 0.5 m or less.

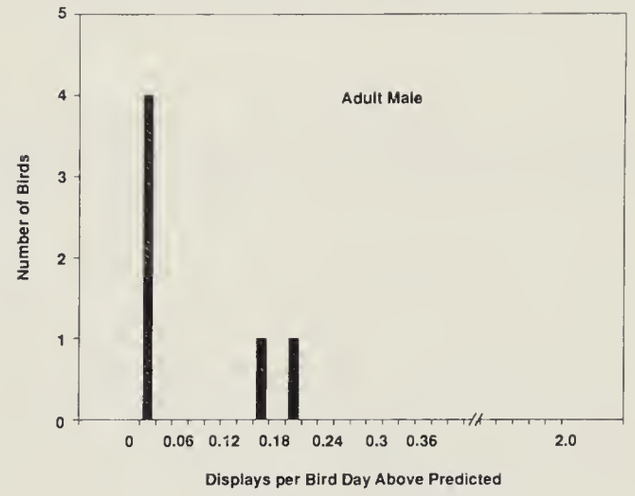
During the time when the feeders were in use, 92 individual birds were observed. The ruffling display was seen in 15 (47%) of 32 juvenile males, nine (43%) of 21 juvenile females, nine (50%) of 18 adult males, and six (29%) of 21 adult females for a total of 39 (42% of all birds). Many birds that attended the feeders frequently were never seen to give the display, although they were involved in agonistic interactions of other types. We could not discern any behavioral or physical differences between displayers and non-displayers.

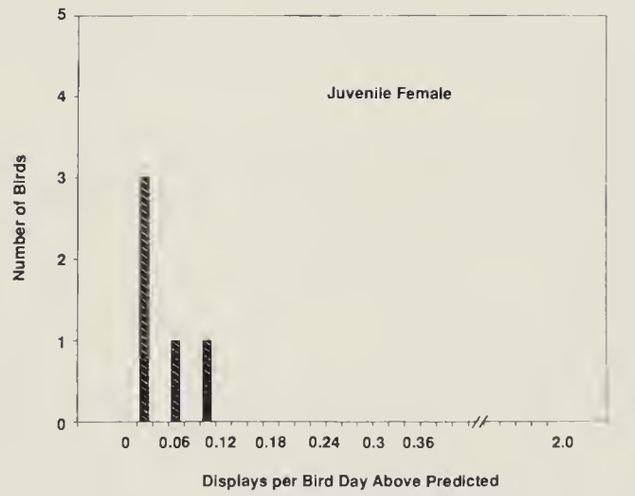
Table 1 lists the age and sex of the displayers and recipients of the encounters in which both individuals were identified by color code (N = 143). A large proportion of the displays were given by juvenile males ($G = 38.0$, df = 1, $P < 0.01$). Conversely, there were no age and sex differences among recipients of the display ($G = 2.27$, df = 3, $P > 0.05$). As some displaying individuals gave the display much more frequently than others (range 1–26, mean ± SE = 4.8 ± 0.84), we needed assurance that our statistical test was not unduly influenced by a few individuals. We prepared a standardized frequency distribution of displays for all birds; this showed that the higher display rate of juvenile males was not due to just a few individuals. As shown in Fig. 2, many juvenile males displayed at much higher frequencies than predicted by their bird-days at feeders, while relatively few of the other age-sex classes did so.

Although usually directed toward conspecifics, chickadees occasionally gave the display toward White-breasted Nuthatches (*Sitta carolinensis*) (one observation for each age and sex category of displayer; not included in Table 1).

The frequency of body ruffling displays was analyzed by month and observation hours and compared with the frequency of all aggressive


Juvenile Male
Number of Birds
0
1
2
3
4
5
0
0.06
0.12
0.18
0.24
0.3
0.36
2.0
Displeys per Bird Dey Above Predicted


Adult Male
Number of Birds
0
1
2
3
4
5
0
0.06
0.12
0.18
0.24
0.3
0.36
2.0
Displays per Bird Day Above Predicted


Juvenile Female
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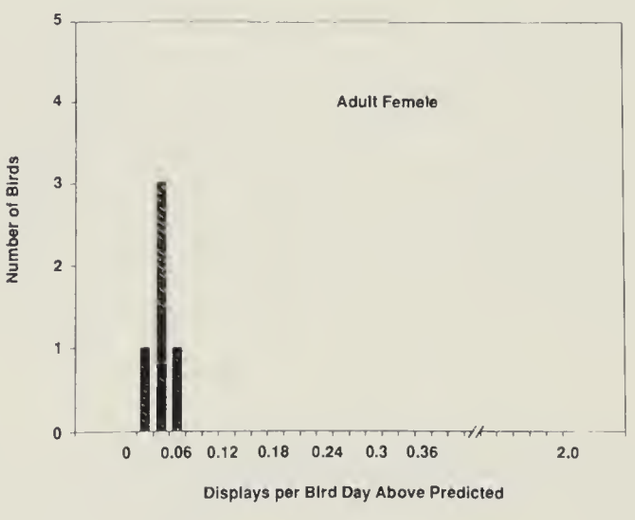
Adult Femele
Number of Birds
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Displays per Bird Day Above Predicted

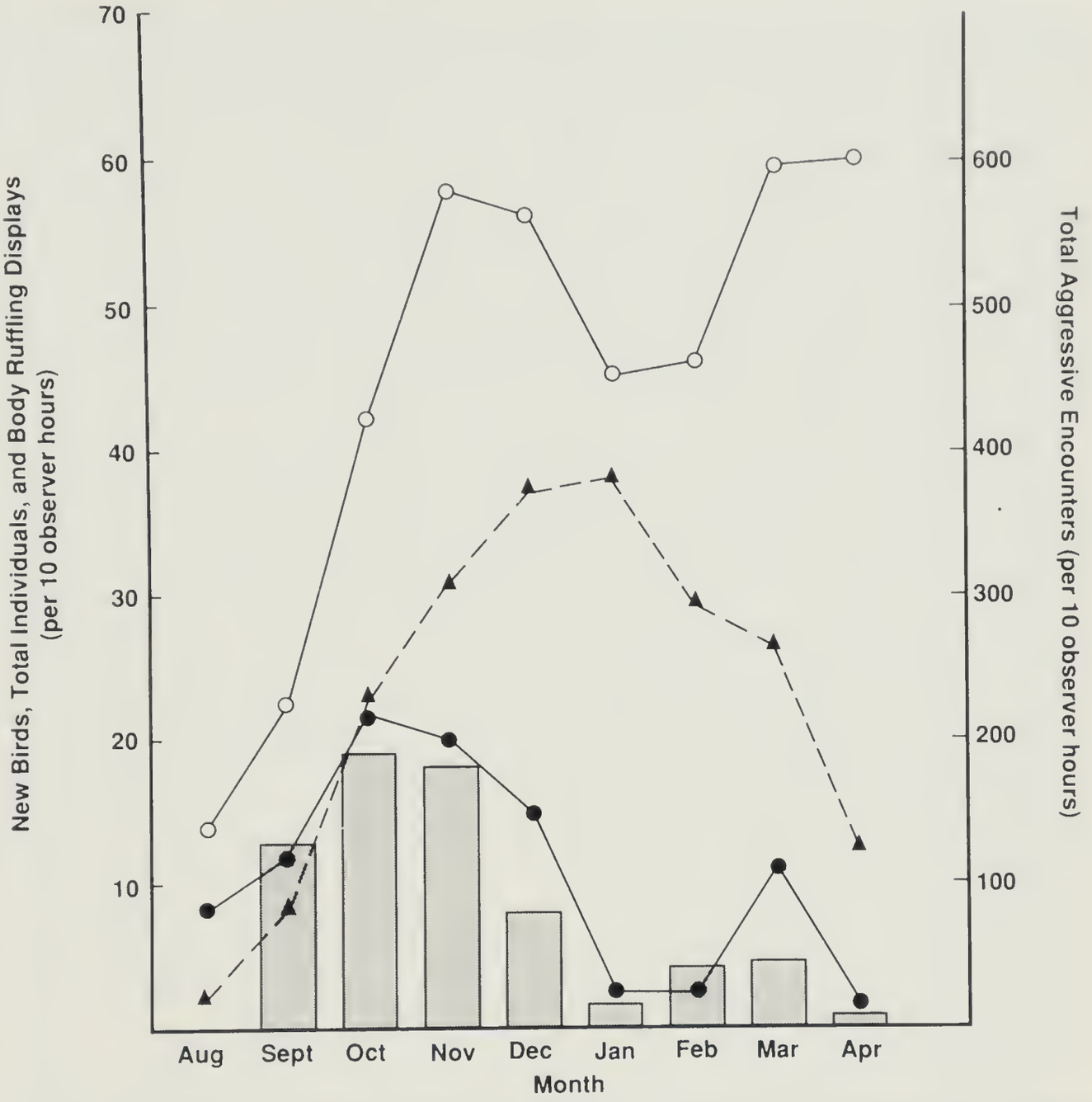

FIG. 3. Relationship of body ruffling displays to new birds, total individuals, and total aggressive encounters. Bars represent body ruffling displays per 10 observer-h. Closed circles represent new birds arriving at the feeders during the month. Open circles represent total individuals using feeders. Dashed line represents aggressive encounters per 10 observer-h.

interactions, the number of new arrivals, and the total number of individuals present at the feeders (Fig. 3). The display was not seen in July or August (in 25 h of observation) but occurred throughout the nonbreeding season, more commonly in the fall (Oct–Dec) than in all other months combined (Aug, Sept, Jan–Apr) ($G = 48.4$, df = 1, $P < 0.001$).

←

FIG. 2. Standardized frequency distributions showing occurrence of ruffling display in relation to bird-days of feeder use. The graph shows only those birds that displayed more frequently than predicted.

Apparently body ruffling occurs infrequently, if at all, on territory during the breeding season. Although we have no systematic data, none of us has ever seen the display at that time during many hours of observation.

We hypothesized that body ruffling was correlated with the arrival of new birds (those appearing for the first time at the feeder within one week of the display). As shown in Fig. 3, the frequency of displays paralleled the number of new birds ($r_s = 0.88$, $P < 0.005$). In displays where the tenure at the feeder of both birds was known (N = 175), 87% involved one newly arrived individual. Conversely, correlation between body ruffling displays and total number of individuals at the feeders was low ($r_s = -0.02$, $P > 0.05$).

Total aggressive interactions analyzed for Fig. 3 included supplanting, Gargle (Ficken et al. 1978), and head-up, as well as one bird waiting for another. The frequency of the body ruffling display was not significantly correlated with these aggressive interactions ($r_s = 0.25$, $P > 0.05$) which are related to winter weather conditions, position in dominance hierarchy, and interflock behavior (Glase 1973).

We tested the hypothesis that body ruffling is a pairbonding display. In the breeding season of 1988, we located 27 territorial pairs in which both birds were accurately identified by color code. Table 2 shows, for these birds, the number of ruffling displays given in fall and winter toward birds with which they eventually mated, compared with displays toward other birds. Encounter possibilities are based on bird-days of exposure to each category. The hypothesis was rejected, as chickadees displayed toward their eventual mates significantly less than expected ($G = 7.24$, df = 1, $P < 0.01$).

The body ruffling display was often accompanied by other acts generally recognized as aggressive. During or immediately following the display, one bird often supplanted another by lunging at it, and in some instances chasing it. In the 201 displays observed, further aggression by the displayer occurred in 47 (23%) and by the recipient in 18 cases (9%). In some cases, a bird approaching another within 0.5 m resulted in one displaying while the other moved away. The recipient of the ruffling display reciprocated with the same display in 24 (12%) of the interactions. The bird giving the ruffling display at a feeder was most likely to win the encounter and win access to the food source. Where the outcome was a distinct win or loss (N = 173), the displayer won access in 102 encounters and the recipient in 71 ($G = 5.58$, df = 1, $P < 0.05$).

DISCUSSION

The body ruffling display seems to exhibit a "typical intensity" (Morris 1957) in that variations in degree of ruffling of feathers are slight. It is

also sometimes a composite signal (Wilson 1975), with other components being wing extension or, more rarely, head lowering, tail fanning, or leaning toward the opponent. The display is rapid and suited to short-range communication.

Although some studies of other parids have suggested that this, or a similar display, is involved in pair formation, this does not seem to be the case in Black-capped Chickadees. Pair formation in this species has been reported to take place in the fall (Smith 1984), but there is no direct evidence for this. Ficken et al. (1981) found that by January birds found later to be paired were associating more closely with each other than with other members of the flock. If body ruffling has a pairbonding function, it would be expected to occur most frequently in the fall or early winter and between prospective mates. The first was indeed the case, but not the second. The display seldom involved birds that were later found to be mated.

An alternative explanation is that the highly seasonal occurence of body ruffling is related to the formation of winter flocks and establishment of dominance hierarchies (S. Haftorn, O. Hogstad, pers. comm.). In late summer, a feeder is visited by adult birds from adjacent territories. Gradually, juvenile birds join the adults and flocks become recognizable. In the fall, feeders are visited by these nearby flocks and later by flocks from more distant areas. Also, individual chickadees, especially juvenile birds, switch with some frequency between flocks and feeders (Smith 1984, Smith and VanBuskirk 1988). These activities result in large numbers of new individuals coming in contact with each other, and there is much intra- and interflock aggression. Juvenile birds not yet established in a flock or dominance hierarchy may utilize body ruffling to win access to food. As winter approaches, attendance at feeders stabilizes, dominance hierarchies are firmly established, birds switch less frequently, and the incidence of body ruffling decreases. In contrast, the frequency of other aggressive interactions continues to increase and peaks in mid-winter when competition for access to food is most intense.

Chickadees use a variety of agonistic behavior patterns, some of which frequently lead to the immediate departure of the opponent. In social species, however, some displays do not necessarily lead to the retreat of the opponent but may increase the actor's ability to have first access to resources (Senar 1990). Body ruffling seems to belong to this category of agonistic displays. The posture is used by juvenile males in the fall as flocks and dominance hierarchies are becoming established. The immediate function is to maintain individual distance or to win access to a food source. Perhaps by increasing apparent size, it helps juveniles compete more effectively for dominance status.

ACKNOWLEDGMENTS

The authors thank J. Reinartz for statistical advice, L. Nelson for his support at the Field Station during the study, and L. Hopwood for his helpful comments on the manuscript. This is publication No. 125 of the Univ. of Wisconsin–Milwaukee Field Station.

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PTILOCHRONOLOGY: INDUCED FEATHER GROWTH IN NORTHERN CARDINALS VARIES WITH AGE, SEX, AMBIENT TEMPERATURE, AND DAY LENGTH

THOMAS C. GRUBB, JR.,[1] THOMAS A. WAITE,[1] AND ARTHUR J. WISEMAN[2]

ABSTRACT.—Growth bars indicate 24-h periods of feather growth. Ptilochronology uses the width of growth bars on an induced feather to monitor avian nutritional condition, the wider the growth bars the better the condition. Because such an interpretation could be confounded if extraneous variables remained uncontrolled, we investigated whether seasonality, temperature, photoperiod, and a bird's age and sex influenced the daily growth of an induced feather. Width of growth bars, and the total length and mass of both an induced feather and the original feather grown from the same follicle during the preceding pre-basic molt varied significantly with the age and sex of Northern Cardinals (*Cardinalis cardinalis*). These same characteristics of induced feathers also varied significantly with season. Despite strong collinearity between ambient temperature and photoperiod, the former appeared to be the more important predictor of feather growth. These results indicate that variation in feather growth due to age, sex, and season of the year must be accounted for in the design of experiments using ptilochronology to examine avian nutritional condition. *Revised 11 Jan. 1991, accepted 13 March 1991.*

The technique termed ptilochronology uses the width of daily growth bars on an induced feather as an index of a bird's nutritional condition (Grubb 1989). Because the plumage coat is important in protection, thermoregulation, and locomotion (Murphy et al. 1988), feather regeneration should proceed as rapidly as possible subject to certain constraints. Such constraints could be exogenous (e.g., food scarcity), endogenous (e.g., allocation of assimilated resources to reproduction), or both. Reduction of feather growth might then be considered a 'compensatory mechanism' (sensu King and Murphy 1985) counterbalancing such constraints. Thus, the reduced growth of an induced feather might indicate a reduction in nutritional condition too minor to cause the net catabolism of body tissues and resulting mass loss that King and Murphy (1985) considered to be the definitive indicators of "nutritional stress."

Ptilochronology depends on two principles, both of which now have empirical support: (1) one growth bar equals 24 hours' growth of the feather (Michener and Michener 1938), and (2) a deficient diet causes a

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reduction in growth bar width (Grubb, in press). However, the interpretation that a reduction in growth bar width indicates a lowering of nutritional condition could be confounded if other factors also influence the rate of feather growth. Recently, Zuberbier and Grubb (unpubl. data) have shown that the rate of daily feather growth in captive White-breasted Nuthatches (*Sitta carolinensis*) on ad libitum food was unaffected by various wind velocities in combination with ambient temperatures well below the thermal neutral zone. Thus, reduction of daily feather growth in birds wintering in cold climates can be more confidently ascribed to a reduction in nutritional condition uncomplicated by any "wind-chill" phenomenon acting at the level of the follicle.

We examined daily growth of induced rectrices of Northern Cardinals (*Cardinalis cardinalis*) in relation to the birds' age and sex, and to the ambient temperatures and daylengths in which the rectrices were regenerated. This sedentary species inhabits old-field communities and the brushy margins of woodlands (Dow 1969a, b). While omnivorous, cardinals maintain a higher percentage of plant food in their diet during winter (88%) than during summer (39%), with spring and autumn intermediate (Martin et al. 1951).

METHODS

At two banding stations (39°00′N, 84°02′W and 39°00′N, 84°03′W) near Cincinnati, Ohio, AJW pulled the outermost right (R6) rectrix from Northern Cardinals during the latter months of 1968, all of 1969, and the early months of 1970. Birds were sexed by plumage color. Age was determined by color of body plumage and bill, retained juvenile primaries and/or secondaries, color and shape of rectrix tips (Scott 1967), skull ossification, or by a combination of these characteristics (Wiseman 1977). AJW then collected the regenerated feather weeks or months later, sometimes retrapping a bird several times and obtaining a sequence of induced R6 rectrices. To reduce the potential impact of uncontrolled variables, we confine this analysis to the first induced R6 rectrix of 186 individual cardinals first caught during 1969. All of these birds had access to supplementary food in the form of sunflower seeds and mixed small grains throughout the year.

As the original and induced rectrices were collected from each bird, they were taped by the rachis to an index card on which were recorded the collection dates of the feathers plus the bird's band number, age and sex. The feathers remained in storage until they were measured by TCG in 1989. During the intervening score of years, several feathers were partially consumed by feather lice. Therefore, while two of the three measures of feather growth we employed for analysis, growth bar width (Grubb 1989) and total feather length, were available for the entire sample, feather mass was obtained (to the nearest 0.1 mg on an analytical balance) for only the 177 pairs of original and induced feathers that had no apparent damage.

We inferred from our unpublished observations of other passerine species that regeneration of the 10 growth bars from which we computed mean daily growth of an induced feather (Grubb 1989) had occurred at about the middle of the 30-day period after the original feather had been pulled. Therefore, to assess the effects of day length and ambient temperature on feather growth, we first determined mean daylength (minutes between sunrise and sunset)

at 40° N (Hoffman 1988) and mean daily maximum, minimum and average temperature (°C) at the Abbe Observatory near Cincinnati (39°09′N, 84°31′W; Anon. 1969) for the 30-day period after each pull date.

Statistical analyses.—We used three-way multivariate analysis of covariance (MANACOVA) to examine whether each of the three measures of induced feather growth in Northern Cardinals was related to age, sex or season (Jan–Apr, May–Aug, Sept–Dec), and whether interaction effects existed among these factors. In this design, the dependent variables were daily growth (mean growth bar width), total length and mass of the induced RC rectrix. The corresponding covariates were daily growth, total length and mass of the original R6 rectrix. We used the MANACOVA procedure because the daily growth, total length and mass of the induced rectrix were related roughly linearly to the daily growth, total length and mass of the original rectrix. Therefore, differences found in any of the three dependent variables between adults and juveniles, between males and females, or among seasons could be partly attributable to differences in the daily growth, total length or mass of the original rectrix. The MANACOVA should have removed this possible source of bias.

The results of the MANACOVA revealed significant covariate effects for all three dependent variables. Therefore, to assess whether the three measures of the growth of original R6 rectrices (daily growth, total length, and mass) might have been age- or sex-specific, we performed two-way analyses of variance on those measures.

To investigate whether photoperiod or air temperature might have been responsible for the seasonal patterns in rectrix regeneration, we first performed stepwise regressions of daily growth (DG_i), total length (TL_i), and mass (M_i) of the induced feather for each of the age-sex classes on several variables, mean day length and mean minimum, maximum and average temperatures, during the 30-day post-pluck period. We also performed the same analyses on the corresponding measures of growth of the original R6 rectrix (DG_o, TL_o, and M_o). The alpha-to-enter and alpha-to-remove were both set at 0.15. This procedure was used only to select a subset model for prediction purposes (see Wilkinson 1989 for rationale). We then used multiple regression analysis to estimate partial regression coefficients for each of the predictors (factors) selected to the subset model by the stepwise procedure. For the results of stepwise and parametric multiple regression analyses to be meaningful, a three-dimensional surface fitted to the relationship among three variables should form a tilted plane with relatively little global flex. Surface plots produced by distance-weighted least-squares smoothing (Wilkinson 1988) revealed pronounced nonplanar relationships among temperature, day length and all three measures of growth for cardinals of all four age-sex classes. In general, feather regeneration tended to be enhanced at high temperatures irrespective of day length, and on short days when temperature was relatively high. Therefore, all of the analyses described above were performed on ranks. This method is usually less powerful than parametric methods, but it circumvents the problem of nonplanar relationships among the variables and its results parallel those of parametric methods (Conover 1980).

RESULTS

The most striking result of the three-way MANACOVA (Table 1) was the significant effect of season for all three measures of rectrix regeneration (Fig. 1), with cardinals tending to regenerate their R6 rectrix most slowly and to the smallest total length and mass during the winter months. The sexes differed significantly in the mean daily growth rate of the induced rectrix. Although statistically significant, the difference between the means for males ($\bar{x} \pm$ SD: 3.33 ± 0.33 mm/day) and females (3.35 ± 0.38 mm/

TABLE 1

RESULTS OF THREE-WAY MANACOVA FOR THREE MEASURES OF THE REGENERATION OF INDUCED R6 RECTRICES (DAILY GROWTH, TOTAL LENGTH, AND MASS) IN NORTHERN CARDINALS[a]

Measure of rectrix growth	Factor	df	*F*	*P*
Daily growth (N = 186)	Age	1, 173	0.443	0.506
	Sex	1, 173	4.014	0.047
	Season	2, 173	12.322	<0.001
	Age*sex	1, 173	0.000	0.991
	Age*season	2, 173	5.605	0.004
	Sex*season	2, 173	2.346	0.099
	Age*sex*season	2, 173	0.272	0.762
	DG_o	1, 173	7.455	<0.001
Total length (N = 186)	Age	1, 173	0.435	0.511
	Sex	1, 173	0.072	0.789
	Season	2, 173	14.978	<0.001
	Age*sex	1, 173	0.016	0.900
	Age*season	2, 173	2.052	0.131
	Sex*season	2, 173	3.104	0.047
	Age*sex*season	2, 173	0.301	0.740
	TL_o	1, 173	89.498	<0.001
Mass (N = 177)	Age	1, 173	0.091	0.764
	Sex	1, 173	1.465	0.228
	Season	2, 173	18.177	<0.001
	Age*sex	1, 173	0.076	0.783
	Age*season	2, 173	2.130	0.122
	Sex*season	2, 173	0.939	0.393
	Age*sex*season	2, 173	0.276	0.759
	M_o	1, 173	27.692	<0.001

[a] The factors are age, sex and season (Jan–Apr, May–Aug, Sept–Dec), and the corresponding covariates are daily growth (DG_o), total length (TL_o) and mass (M_o) of the original R6 rectrices.

day), irrespective of age and season, was small (see Fig. 2). Two significant interaction effects also emerged. First, differences in the daily growth rate of the induced R6 rectrix in juveniles and adults varied across seasons (Fig. 3a). In particular, juveniles tended to regenerate their rectrix more slowly than adults during the May–August period. Second, differences in the total length of the induced R6 rectrix in males and females varied across seasons (Fig. 3b). While females grew a longer induced rectrix than did males during the May–August period, they grew a shorter one during the other times of year.

It seems probable that the significant covariate effects for all three measures of rectrix regeneration (Table 1) were largely the result of dif-

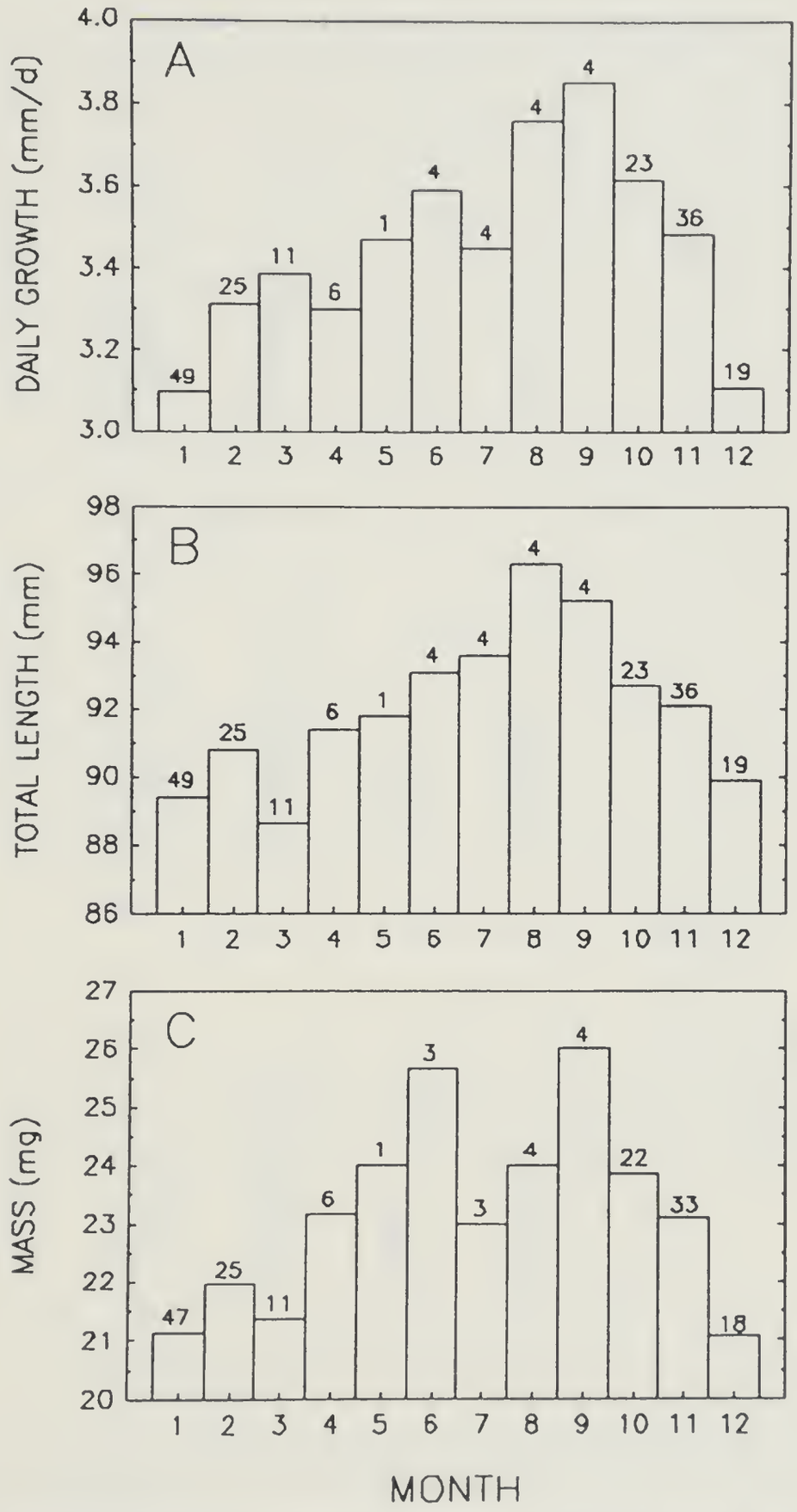

FIG. 1. Regeneration of R6 rectrices in Northern Cardinals throughout the year (Jan–Dec); the width of daily growth bars on the induced rectrix (A), and the total length (B) and mass (C) of the induced rectrix. The bars indicate the means, and the numerals represent the sample sizes.

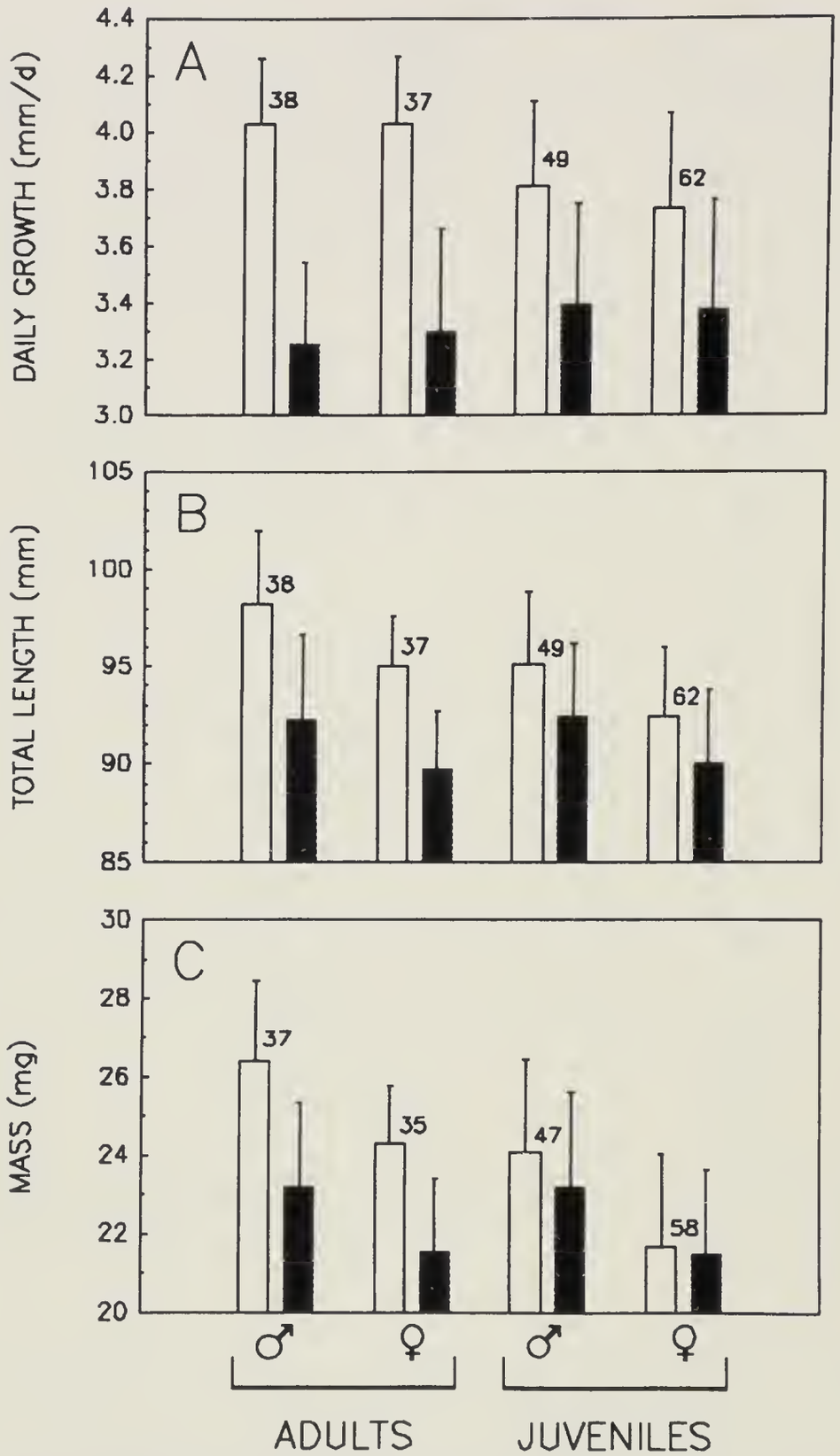

FIG. 2. Growth of original (open bars) and induced (filled bars) R6 rectrices in Northern Cardinals of different age-sex classes; the width of daily growth bars of the original and induced retrices (A), the total length (B) and mass (C) of the original and induced rectrices. The bars represent the means and the vertical lines indicate one SD. The numerals correspond to the number of cardinals of a given age-sex class from which both an original and an induced rectrix were taken.

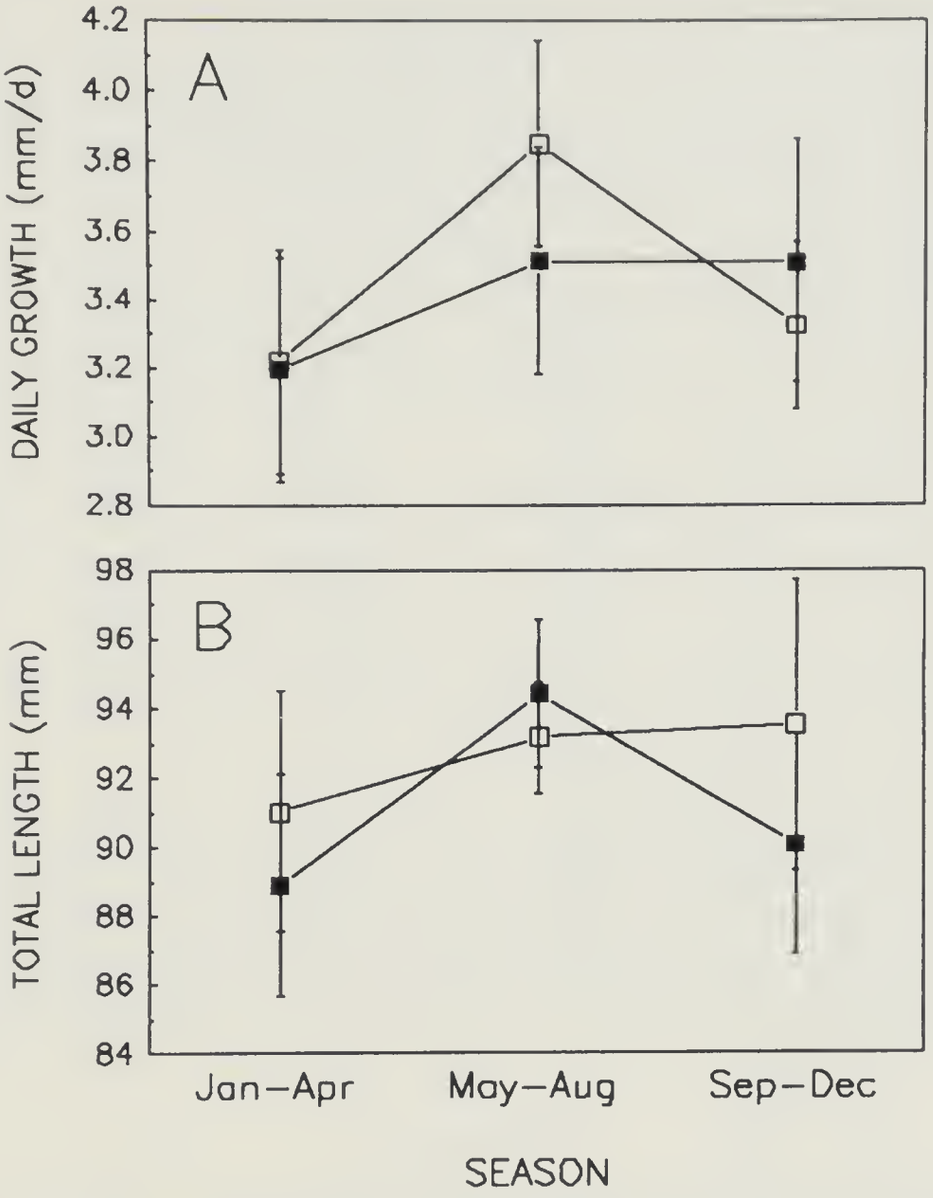

FIG. 3. (A) Mean width of daily growth bars on induced R6 rectrices grown by adult (open squares) and juvenile Northern Cardinals (filled squares) during different seasons (Jan–Apr, May–Aug, Sept–Dec). (B) Mean total length of induced R6 rectrices grown by male (open squares) and female cardinals (filled squares) during different seasons. Vertical lines indicate ±SD.

ferences among the age-sex classes of cardinals. Fig. 2 shows the measures of growth of the original and induced R6 rectrices for the four age-sex classes. Two-way analysis of variance (Table 2) indicated that adults grew their original rectrix faster and to a greater total length and mass than did juveniles. In addition, males tended to grow a longer and heavier induced rectrix than did females.

Multiple regression analysis (Table 3) showed that at least one measure of air temperature was a significant predictor of all three measures of rectrix regeneration in cardinals of all four age-sex classes. Although a negative partial correlation emerged between M_i and T_{max} in juvenile females, the positive sign of the 12 remaining partial regression coefficients

TABLE 2
RESULTS OF TWO-WAY ANALYSIS OF VARIANCE FOR THREE MEASURES OF THE GROWTH OF ORIGINAL R6 RECTRICES IN NORTHERN CARDINALS

Measure of rectrix growth	Factor	df	*F*	*P*
Daily growth (N = 186)	Age	1, 182	34.765	<0.01
	Sex	1, 182	0.703	0.403
	Age*sex	1, 182	0.818	0.367
Total length (N = 186)	Age	1, 182	30.685	<0.001
	Sex	1, 182	32.135	<0.001
	Age*sex	1, 182	0.305	0.582
Mass (N = 177)	Age	1, 173	55.249	<0.001
	Sex	1, 173	46.612	<0.001
	Age*sex	1, 173	0.259	0.611

indicates that the cardinals regenerated their R6 rectrix at a faster daily rate and to a greater total length and mass at higher temperatures. In addition, day length was a significant predictor of all three measures of rectrix regeneration in juvenile males and a significant predictor of DG_i in juvenile females. Juvenile cardinals had enhanced rectrix regeneration during *shorter* days.

DISCUSSION

Our results suggest that several factors other than a bird's nutritional condition may influence the rate at which a feather is regenerated (Table 1). Aside from differences that might have been expected due to age- and sex-specific variation in such factors as body size, social dominance, and foraging efficiency (e.g., males may have had an advantage over females during winter; see Fig. 3b), there was a pronounced seasonal pattern in feather growth. All four age/sex categories displayed an annual cycle with more rapid growth in summer than in winter.

Our study appears to be the first to relate temperature and daylength to nonmolt feather regeneration, but several workers have examined the influence of temperature and photoperiod during the pre-basic molt. In general, the onset of molt occurs earlier in birds exposed to longer photoperiods (e.g., Blackmore 1969, Chilgren 1978), but Chilgren found that at 20°C, molting captive White-crowned Sparrows (*Zonotrichia leucophrys*) grew out a primary feather at statistically indistinguishable daily rates under 8:16 and 4:20 L:D regimes. He concluded that growth rates of individual feathers during the molting season do not seem to vary with photoperiod as long as some presently undefined maximum length of daylight is available.

TABLE 3

RESULTS OF MULTIPLE REGRESSION OF DAILY GROWTH (DG_i), TOTAL LENGTH (TL_i) AND MASS (M_i) OF INDUCED R6 RECTRICES IN NORTHERN CARDINALS OF FOUR AGE-SEX CLASSES ON THOSE PREDICTORS (FACTORS) SELECTED BY A PRIOR STEPWISE REGRESSION PROCEDURE[a]

Age-sex class	Measure of rectrix regeneration	Factor	Partial rank regression coefficient	*P*	Multiple R^2	N	df
Adult males	DG_i	T_{max}	0.339	0.039	0.114	38	1, 36
	TL_i	TL_o	0.836	<0.001	0.654	38	2, 35
		T_{max}	0.408	<0.001			
	M_i	M_o	0.729	<0.001	0.608	37	3, 33
		T_{min}	0.625	<0.001			
		Day length	−0.180	0.144			
Adult females	DG_i	T_{mean}	0.483	0.003	0.259	37	2, 34
		DG_o	0.294	0.058			
	TL_i	TL_o	0.355	0.004	0.574	37	2, 34
		T_{mean}	0.599	<0.001			
	M_i	T_{min}	0.632	<0.001	0.509	35	2, 32
		M_o	0.314	0.018			
Juvenile males	DG_i	T_{min}	0.885	<0.001	0.360	49	2, 46
		Day length	−0.600	0.001			
	TL_i	TL_o	0.385	0.002	0.394	49	3, 45
		Day length	−0.562	0.002			
		T_{min}	0.708	<0.001			
	M_i	M_o	0.210	0.103	0.332	47	3, 43
		Day length	−0.544	0.015			
		T_{max}	0.879	<0.001			
Juvenile females	DG_i	DG_o	0.269	0.009	0.458	62	3, 58
		Day length	−0.325	0.033			
		T_{min}	0.892	<0.001			
	TL_i	TL_o	0.639	<0.001	0.611	62	2, 59
		T_{min}	0.560	<0.001			
	M_i	M_o	0.415	<0.001	0.552	58	3, 54
		T_{max}	−0.847	0.043			
		T_{min}	1.446	0.001			

[a] See methods for details. All analyses were performed on ranks.

Our results suggest that ambient temperature was a more important predictor of feather growth rate than was photoperiod, particularly in adult cardinals (Table 3). The negative correlations between photoperiod and feather growth in juveniles suggest that they were less well nourished than adults (Fig. 3a) during the long summer days soon after fledging. Later on, they were presumably better at finding food and so actually were in better nutritional condition during the shorter days of autumn. However, because of strong collinearity between day length and temperature,

one must be cautious in assessing the relative importance of these two variables in explaining variation in any of the measures of rectrix regeneration. Similarly, inferences based on which of the three temperature variables entered the model for any particular measure of growth should be made cautiously.

If Chilgren (1978) was correct in stating, "Growth rates of individual feathers appear to be unalterable under conditions of adequate nutrition and some brief, but undefined photopheriod," why did our cardinals regenerate a longer, heavier rectrix faster in warmer weather? Perhaps their nutrition may not have been equally "adequate" throughout the year. Existence metabolism is much higher in winter than in summer for resident temperate-zone birds (e.g., Munzinger 1974). Furthermore, during the winter, such birds must deal with a diminishing food supply. Thus, less net energy may be available for feather growth in the colder, leaner months of the year. Support for this idea comes from a study of White-breasted Nuthatches regenerating induced rectrices in controlled temperatures of −15, −5, or +5°C (Zuberbier and Grubb, unpubl. data). Under conditions of ad libitum food, feathers grown over this 20°C range of temperatures did not differ in daily growth. This explanation based on differential nutritional condition is somewhat confounded, however, because throughout the year the cardinals we studied could have had access to supplementary food at the trapping sites. Unfortunately, the extent to which individual birds used this supplementary food is unknown. Had there been no extra food, the influence of ambient temperature on feather growth might have been even more substantial.

The evidence from studies of molt concerning the influence of temperature on feather growth is sparse and conflicting. Warmer temperatures advanced the molt in White-crowned Sparrows (Chilgren 1978), but delayed it in Chaffinches (*Fringilla coelebs*) (Gavrilov and Dolnik 1974; cited by Chilgren 1978). Low temperature (5°C) reduced the overall duration of molt in White-crowned Sparrows (Chilgren 1978), but we have found no information on whether ambient temperature affects the daily growth of individual feathers during the molt.

In conclusion, these results limit the freedom with which ptilochronology can be used to study various aspects of avian behavior and ecology (Grubb 1989). Variation in feather growth due to age, sex, or season of the year must be accounted for in the design of experiments (e.g., Grubb 1989, Waite 1990, Grubb and Cimprich 1990).

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FOREST HABITAT LOSS, FRAGMENTATION, AND RED-COCKADED WOODPECKER POPULATIONS

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ABSTRACT.—Loss of mature forest habitat was measured around Red-cockaded Woodpecker (*Picoides borealis*) cavity tree clusters (colonies) in three National Forests in eastern Texas. Forest removal results in a loss of foraging habitat and causes habitat fragmentation of the remaining mature forest. Habitat loss was negatively associated with woodpecker group size in small populations that had relatively isolated clusters but not in a larger, more dense population. Cutting patterns also may affect the amount of foraging habitat available to a family group if the group is forced to go through the territories of other groups to access suitable foraging habitat. Habitat loss may affect woodpecker group size by causing an insufficiency of foraging habitat and dispersal-demographic problems. *Received 15 Jan. 1991, accepted 15 April 1991.*

Forest loss and fragmentation and its effects on wildlife have become an increasing concern of scientists, managers, and environmental groups over the past several decades (Harris 1984, Wilcove 1989). Historically, the effects of fragmentation are best known from theory and studies of insular biology (Preston 1962a, b; MacArthur and Wilson 1967). These and subsequent studies (Diamond 1973, 1976) examined the effects of island size and isolation on species richness and extinction rates. This concept was extended to the sizes of habitat fragments necessary to maintain species in preserves and woodland fragments (Diamond and May 1976, Galli et al. 1976, Wilcox 1980, Rosenberg and Raphael 1986).

In addition to problems created by size of forest fragments (Robbins et al. 1989) and dispersal distances between patches, fragmentation within a species home range may have detrimental effects other than simple loss of usable habitat. In mature forest species with large home ranges, dispersing young may have greater difficulty in finding a mate if numerous or extensive patches of nonforest exist within the general forest landscape. Two species that may suffer from this problem are the Spotted Owl (*Strix occidentalis*) and the Red-cockaded Woodpecker (*Picoides borealis*). Both species often have low-density populations with relatively isolated breeding units (Forsman et al. 1984, Ligon et al. 1986, Conner and Rudolph 1989). Habitat patchiness and fragmentation have been predicted to cause dispersal problems within forest habitat in Spotted Owls and other rare species (Lande 1988, Simberloff 1988, Doak 1989).

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Conner and Rudolph (1989) made a preliminary investigation into the effects of forest loss, isolation, and fragmentation on group size in Red-cockaded Woodpeckers while studying population declines in Texas. Analyses indicated that woodpecker group size decreased as forest removal within a 400-m radius of active clusters (colonies, see Walters et al. 1988) increased. Although a group size decline could be caused by a reduction in foraging habitat, foraging areas available in the study were well above minimum requirements described in the recovery plan (USFWS 1985).

In this study, we evaluate relationships between Red-cockaded Woodpecker group size and measures of forest habitat loss and fragmentation in three National Forests in eastern Texas. Our study focuses on populations that are small, have relatively isolated family groups, and occupy a range of nonfragmented to highly fragmented habitat. These small populations are compared to a larger, more dense population. We examine and test the effects of forest loss (foraging habitat insufficiency) and forest fragmentation on Red-cockaded Woodpecker family group size. If group size is related to habitat loss, what is the cause of this relationship? Several hypotheses were formulated to explore this question: (1) If fragmentation is affecting female dispersal for mate replacement, habitat fragmentation around single male clusters should be greater than fragmentation around clusters with only breeding pairs; (2) If habitat loss (foraging insufficiency) is affecting woodpecker group size, habitat loss around clusters with only breeding pairs should be greater than habitat loss around clusters with breeding pairs and helpers. As an additional test to evaluate the effects of fragmentation vs foraging insufficiency on family group size, we compared small and large populations; (3) If habitat loss is affecting foraging sufficiency and fragmentation is not affecting dispersal, woodpecker group size should be a function of habitat loss in both large and small populations.

METHODS

We studied Red-cockaded Woodpeckers in the Angelina (ANF), Davy Crockett (DCNF), and Sam Houston (SHNF) National Forests in eastern Texas. Red-cockaded Woodpeckers on the ANF (62,423 ha) are found primarily in longleaf pine (*Pinus palustris*) habitat (14 active clusters) on the southern portion of the forest, while eight additional clusters are in loblolly (*P. taeda*)—shortleaf (*P. echinata*) pine habitat on the northern portion of the ANF. The northern eight active clusters are isolated from the other active clusters by a distance of more than 34 km and the 4+ km wide Sam Rayburn Reservoir. The DCNF (63,923 ha) is 32 km west of the ANF and primarily loblolly and shortleaf pine forest. Less than 1% of the DCNF is primarily longleaf pine. Active Red-cockaded Woodpecker clusters are primarily located in the northern half of the forest with two active clusters relatively isolated (26 km distant) in the southern extreme of the forest. The SHNF (65,218 ha) is about 30

km south of DCNF. Loblolly pine is the predominant pine species, although shortleaf pine is present in most stands and predominates on the drier sites. The 24 active Red-cockaded Woodpecker clusters in the eastern portion of the SHNF (San Jacinto Ranger District) are sparsely distributed with greater distances between clusters than in the western portion of the forest. The Raven Ranger District has a relatively large population of Red-cockaded Woodpeckers with more than 114 active clusters in the western portion of the SHNF. About 90 active clusters constitute a dense population in a portion of the Raven Ranger District where there is one active cluster per 389 ha of total forest area. Sparse populations in the rest of the SHNF and the ANF and DCNF average one active cluster per 2300 ha of total forest area.

Dawn and dusk visits were made to all known active clusters in the ANF and DCNF between March–June 1987 and late December 1987--June 1988 in the SHNF to determine the number of woodpeckers in each woodpecker family group. Ideally, group size in the SHNF should have also been measured during March and June when group size is lowest. A longer field season was necessary because of the large population size in the SHNF. Also, most mortality of young occurs during the first several months post fledging. If any bias is present, it should be distributed throughout the SHNF and not influence mathematical relationships. Location of each active and inactive cluster was determined on aerial photographs taken November–December 1986. Circles of 400 m and 800 m radii were drawn around clusters on xerographic copies of the aerial photographs (3.2 cm/km). A 400 m radius normally will include all cavity trees within a cluster, and an 800 m radius normally will include all foraging habitat used by a family group (USFWS 1985). All nonforest habitat (forest removal) including permanent private openings and lakes, clearcut stands, southern pine beetle treatment cuts, and pine plantations less than 20 years old >1.5 ha in area (see Conner and Rudolph 1989) were delineated within these two radii, cut out, and measured on a digital electronic area meter (to nearest 0.01 cm^2). Seed-tree and shelterwood regeneration areas where residual pines were still present were considered to be forest habitat because of the Red-cockaded Woodpecker's use of open pine savanna habitat (Patterson and Robertson 1981) and their frequent use of seed-tree and shelterwood areas (Conner et al. 1991). The number of separate cuts within the 400 and 800 m radii of each cluster was also counted. As an additional measure of habitat loss, an angular measure of nonmature forest habitat as viewed from the cluster center out to 800 m was summed (Fig. 1). Thus, if a cut was close to a cluster center, a larger angle would be required to view the lateral edges of the cut than for a similar cut that was farther away. Of these variables, the angular sum of nonmature habitat and the number of cuts may be better measures of fragmentation, whereas the percent of forest removal may be a better measure of habitat loss. Clearly, it is difficult to separate these two landscape characteristics. Also, the number of active clusters within 2 km of each cluster was also determined as a measure of isolation.

Active woodpecker clusters were initially divided into small ($\leq$two woodpeckers) and large ($>$two woodpeckers) family groups to test for relationships of group size with habitat loss. Variables measuring habitat loss and isolation were compared between large and small groups with *t*-tests. Separate variance estimates were used if variances between analysis groups were significantly different (SPSSX 1986). Spearman rank correlation was used to examine relationships between actual woodpecker group size and habitat variables. Logistic regression was used to determine if group size (small vs large) and cluster status (active and inactive) in small Red-cockaded Woodpecker populations were a function of habitat loss (Dixon et al. 1985).

Active clusters were then divided into three groups (single males, breeding pairs, and breeding pairs plus helpers) and compared to determine the relative contribution of fragmentation vs habitat loss to woodpecker group size. Habitat around single male clusters in

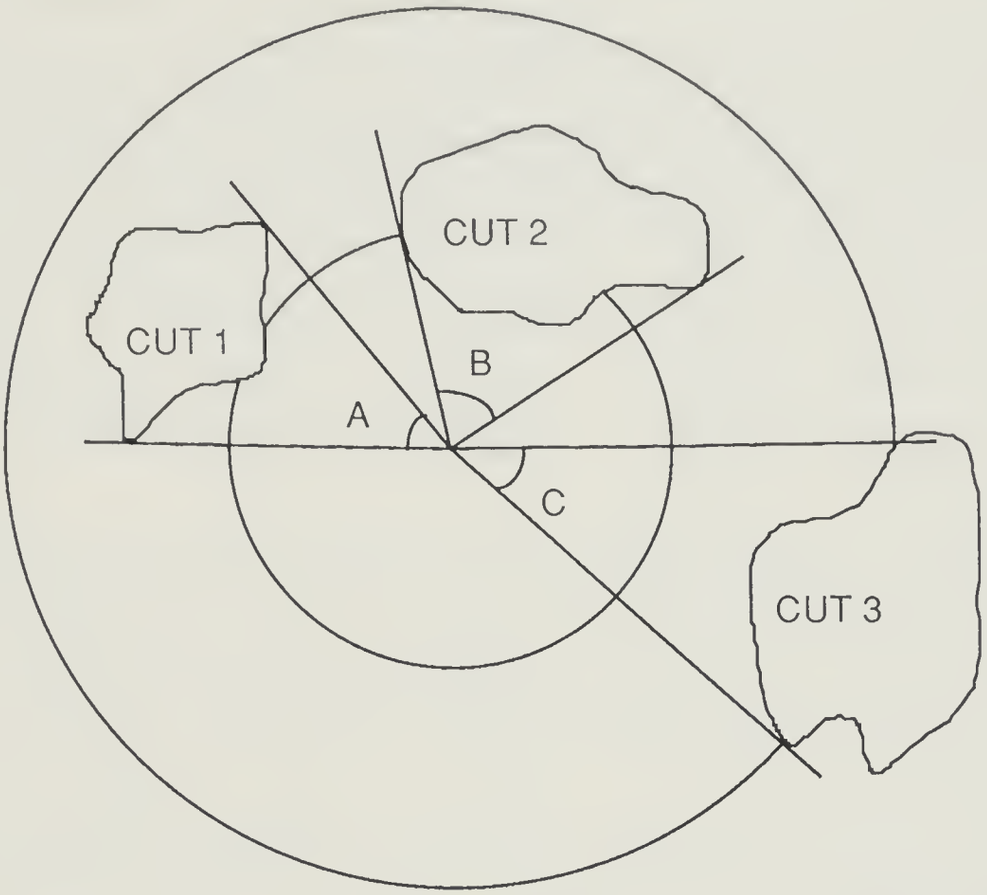

FIG. 1. Method used to measure the angular sum (ANGSUM) of nonforest habitat (cut areas) around active Red-cockaded Woodpecker clusters in eastern Texas. The sum of angles A, B, and C would yield the measurements for this particular cluster that would be at the center of the circles. The inside circle's radius is 400 m and the outside circle's radius in 800 m.

small populations was compared to habitat around clusters with only breeding pairs to determine if the ability of dispersing young female Red-cockaded Woodpeckers is hampered by habitat fragmentation. Habitat around clusters with breeding pairs was compared with habitat around clusters with pairs and helpers to determine if habitat loss affects the ability of an area to support woodpeckers. Habitat around clusters with only breeding pairs was compared to habitat around clusters with breeding pairs and helpers on both small and large populations to test whether fragmentation-dispersal or foraging insufficiency was most associated with woodpecker group size. Group pairs were compared with *t*-tests.

RESULTS

As measures of forest fragmentation and habitat loss increased, woodpecker group size in small populations decreased. The number of cuts within 400 m (NCUT 4), the angular sum of cuts within 800 m (ANGSUM), percentage of nonforest area within 400 m (PERCUT4), and 800 m (PERCUT8), were significantly higher in habitat around Red-cockaded Woodpecker clusters that had small group sizes than around large groups (Table 1). Small woodpecker groups were not significantly more isolated (ISOL2KM) than large groups in the small populations (Table 1). The

TABLE 1

COMPARISONS OF SMALL (≤TWO WOODPECKERS, N = 49) AND LARGE (>TWO WOODPECKERS, N = 19) RED-COCKADED WOODPECKER GROUPS ON THREE NATIONAL FORESTS IN EASTERN TEXAS USING MEASURES OF FOREST FRAGMENTATION WITH A *T*-TEST ON DATA FROM SMALL, SPARSE POPULATIONS

Variable	Code	Small group mean (SE)	Large group mean (SE)	*t*	Two-tailed *P*
No. cuts within 400 m	NCUT4	2.1 (0.20)	1.3 (0.3)	2.02	0.047
No. cuts within 800 m	NCUT8	7.0 (0.5)	5.5 (0.9)	1.45	0.153 ns[a]
Angular sum of cuts within 800 m	ANGSUM	226.0 (13.7)	156.8 (25.7)	2.55	0.013
Percentage of nonforest area within 400 m	PERCUT4	24.8 (2.5)	13.3 (4.5)	2.36	0.021
Percentage of nonforest area within 800 m	PERCUT8	26.9 (2.4)	16.2 (4.1)	2.33	0.023
No. active clusters within 2 km	ISOL2KM	2.6 (0.3)	2.3 (0.6)	0.67	0.507 ns[a]

[a] Not statistically significant.

number of woodpeckers per group (NRCWS) decreased significantly as the amount of fragmentation and habitat loss within 400 m and 800 m of active clusters increased (Table 2). Logistic regression indicated that woodpecker group size was a function of the angular sum of forest cuts less than 20 years old in small woodpecker populations ($\chi^2 = 4.73$, $P = 0.030$).

An average of 11.9 ± 10.4 (SD) ha of forest had been removed from the 50-ha area within 400 m of woodpecker clusters and 53.1 ± 37.1 (SD) ha from the 201-ha area within 800 m of woodpecker clusters in our small population study areas (N = 68). In the Angelina National Forest, private inholdings accounted for less than 12% of land area within 400 m of active woodpecker clusters; however, about 49% of forest removal within 400 m of active clusters had occurred on private lands.

A logistic regression comparing active (N = 79) and inactive (N = 90) clusters indicated that cluster status (active vs inactive) was a function of the percentage of nonforest habitat (<20 years old) within 800 m of clusters ($\chi^2 = 4.02$, $P = 0.045$) in small populations. Analyses with small populations and the dense, large population combined indicated that isolation (ISOL2KM, $t = 3.14$, df = 304, $P = 0.002$) and percentage of forest removal within 800 m (PERCUT8, $t = 2.39$, df = 304, $P = 0.017$) were significantly higher around inactive clusters than active clusters.

TABLE 2

CORRELATIONS (r_s) OF MEASURES OF FOREST FRAGMENTATION WITH RED-COCKADED WOODPECKER GROUP SIZE

Variables[a]	NCUT4	NCUT8	ANGSUM	PERCUT4	PERCUT8	ISOL2KM
NRCWS[b]	−0.24	−0.12	−0.28	−0.30	−0.24	0.03
P	0.025	0.157	0.010	0.007	0.026	0.400

[a] See Table 1 for codes.
[b] NRCWS—numbers of woodpeckers per family group (1–5), N = 68.

A comparison of forest habitat loss variables between small and large woodpecker groups in the densely populated portion of the Raven Ranger District revealed that only the number of cuts within 800 m of active clusters (NCUT8) was significantly greater around small family groups (Table 3). Similarly, only NCUT8 was significantly correlated to the number of woodpeckers per group (NRCWS, $r_s = -0.20$, $P = 0.033$).

There were major significant differences between all measures of habitat loss and cluster isolation around dense populations in the Raven Ranger District and the sparse populations in the rest of the National Forest study areas (Table 4). Surprisingly, cutting was significantly more extensive around active clusters from the dense population than around clusters from sparse populations. There were nearly twice as many active clusters within 2 km of each active cluster in the dense population when compared to the sparse populations (Table 4).

In small, sparse populations, comparisons between clusters with only breeding pairs and clusters with breeding pairs and helpers revealed that

TABLE 3

COMPARISON OF SMALL (≤TWO WOODPECKERS, N = 46) AND LARGE (>TWO WOODPECKERS, N = 35) RED-COCKADED WOODPECKER GROUPS IN A DENSE POPULATION IN A PORTION OF THE RAVEN DISTRICT OF THE SAM HOUSTON NATIONAL FOREST

Variable code[a]	Small groups mean (SE)	Large groups mean (SE)	*t*	Two-tailed *P*
NCUT4	3.3 (0.2)	2.7 (0.2)	1.90	0.06 ns
NCUT8	11.2 (0.5)	9.5 (0.4)	2.39	0.01
ANGSUM	285.8 (10.4)	288.3 (9.3)	0.17	0.86 ns
PERCUT4	36.9 (2.9)	36.7 (3.2)	0.04	0.97 ns
PERCUT8	38.4 (2.4)	39.7 (2.8)	0.34	0.73 ns
ISOL2KM	5.0 (0.4)	4.2 (0.5)	1.14	0.25 ns

[a] See Table 1 for codes.

TABLE 4

COMPARISONS OF FOREST FRAGMENTATION AND HABITAT LOSS VARIABLES BETWEEN ACTIVE CLUSTERS IN SMALL, LOW DENSITY RED-COCKADED WOODPECKER POPULATIONS (N = 68) IN THE ANGELINA, DAVY CROCKETT AND EASTERN PORTION OF THE SAM HOUSTON NATIONAL FORESTS AND A LARGER, RELATIVELY HIGH DENSITY POPULATION (N = 81) IN A PORTION OF THE RAVEN RANGER DISTRICT OF THE SAM HOUSTON NATIONAL FOREST

Variable code[a]	Sparse population mean (SE)	Dense population mean (SE)	*t*	Two-tailed *P*
NCUT4	1.9 (0.2)	3.0 (0.2)	5.14	<0.001
NCUT8	6.5 (0.5)	10.4 (0.4)	6.53	<0.001
ANGSUM	206.7 (12.7)	286.9 (7.1)	5.51	<0.001
PERCUT4	21.6 (2.3)	36.8 (2.2)	4.86	<0.001
PERCUT8	24.0 (2.1)	38.9 (1.8)	5.38	<0.001
ISOL2KM	2.5 (0.2)	4.7 (0.3)	5.47	<0.001

[a] See Table 1 for codes.

habitat within 400 and 800 m of pairs with helpers had significantly less forest removal (Table 5). Although habitat around breeding pairs was not significantly different from habitat around single male clusters, means for percentage forest removal and angular sum of cuts were greater for single male clusters. Single male clusters were significantly more isolated than clusters with only breeding pairs (Table 5). There was no significant difference in the isolation of clusters with only breeding pairs and clusters with breeding pairs and helpers.

In the large population in the Raven Ranger District, habitat loss around clusters with only a breeding pair was not significantly different from habitat loss around clusters with breeding pairs and helpers (ANGSUM, $t = 0.16$, $P = 0.87$; PERCUT4, $t = 0.18$, $P = 0.85$; PERCUT8, $t = 0.19$, $P = 0.84$).

Fragmentation appears to have affected a woodpecker group's access to foraging habitat by forcing access routes to go through the territories of adjacent woodpecker groups (Fig. 2). Woodpeckers from cluster 5 in Fig. 2 were forced to forage in the territories of clans from clusters 3, 4, and 6 as a result of cutting that occurred 3–5 years ago. Cluster 5 became inactive during the fall or early winter 1989. All active clusters in Figure 2 have adequate foraging habitat (>51 ha, and >6350 pine stems >26 cm DBH within 800 m) as outlined in the recovery plan (USFWS 1985) and the U.S. Forest Service Red-cockaded Woodpecker management guidelines (USFS 1985). Cluster 2 has 70.3 ha of foraging habitat, cluster 3 has 65.4 ha, and clusters 4, 5, and 6 each have 54.4 ha of nonoverlapping foraging habitat. Woodpeckers from clusters 4 and 6 now frequently forage

TABLE 5

PAIRWISE *T*-TEST COMPARISONS OF THREE RED-COCKADED WOODPECKER GROUP SIZES (SINGLE MALE [SM], BREEDING PAIR [BP], AND BREEDING PAIR PLUS HELPERS [BPH]) WITH MEASURES OF FOREST FRAGMENTATION AND HABITAT LOSS IN THREE NATIONAL FORESTS IN EASTERN TEXAS USING DATA FROM SMALL SPARSE POPULATIONS[a]

Variable	Code	SM mean (SE) N = 15	*t*	*P*	BP mean (SE) N = 34	*t*	*P*	BPH mean (SE) N = 19
No. cuts within 400 m	NCUT4	2.3 (0.4)	0.68	0.50	2.0 (0.2)	1.70	0.09	1.3 (0.3)
No. cuts within 800 m	NCUT8	4.9 (0.8)	0.06	0.95	4.9 (0.5)	0.93	0.35	4.2 (0.6)
Angular sum of cuts within 800 m	ANGSUM	237.8 (26.8)	0.54	0.59	220.9 (16.0)	2.11	0.04	156.8 (25.7)
Percentage of non-forest area within 400 m	PERCUT4	26.8 (4.7)	0.52	0.60	23.9 (3.0)	1.98	0.05	13.3 (4.5)
Percentage of non-forest area within 800 m	PERCUT8	27.1 (5.1)	0.05	0.96	26.9 (2.6)	2.17	0.03	16.2 (4.1)
No. active clusters within 2 km	ISOL2KM	1.8 (0.3)	2.47	0.01	2.9 (0.3)	1.22	0.23	2.3 (0.5)

[a] Group sizes (SM vs BP and BP vs BPH) were compared using two-tailed *t*-test.

FIG. 2. An example of habitat fragmentation (Federal and private lands) around active Red-cockaded Woodpecker clusters in a National Forest in eastern Texas. Cluster 5 recently became inactive most likely as a result of fragmentation forcing the family group to forage in the territories of groups 3, 4, and 6.

near or within the vacated area of cluster 5. The loss of cluster 5, while surrounded by three active clusters, suggests that foraging habitat was insufficient.

DISCUSSION

Woodpecker group size and cluster status were significantly associated with forest removal for small, sparse Red-cockaded Woodpecker populations. As the amount of forest removal increased, woodpecker group size and the number of active clusters decreased. Isolation and forest removal within 800 m of clusters were significantly associated with cluster inactivation in both large and small populations combined. Our measures of forest loss had little or no relationship with group size in our dense population study area, which suggests that small populations are more vulnerable to forest removal than larger, dense populations. Data presented by Wood et al. (1985) contrast with our observations. In the Wood et al. (1985) study up to 37% of the annual territory of Red-cockaded Woodpecker groups was clearcut without any negative effect on the numbers of nestlings or their survival in the nesting period immediately following clearcutting. The population studied by Wood et al. may have been somewhat larger than the small populations in our study. In our study, group size was not affected by our measures of habitat loss in large populations but was affected in small populations. These results would

be expected if habitat loss is affecting dispersal. If habitat loss affected foraging sufficiency, an effect on group size should appear in both small and large populations; it did not.

If an insufficiency of foraging habitat were the cause of small group size, habitat around clusters with only breeding pairs might be expected to have significantly more forest loss than habitat around clusters with larger groups. Forest loss was greater around clusters with only breeding pairs supporting the hypothesis that habitat loss caused an insufficiency of foraging habitat. However, a portion of the relationship could still be related to the effect of forest fragmentation on female dispersal. Our angular sum measurement, which is more a measure of fragmentation than habitat loss, was greater around clusters with only breeding pairs than clusters with larger family groups.

Habitat loss causing fragmentation could affect breeding frequency if it interferes with the ability of unmated females to find an active group that has lost its breeding female. Fragmentation may reduce the contact between groups necessary for young females to take advantage rapidly of such openings. Any delay in the replacement of a mate would decrease group size in the long run, because no young would be produced during the years when a breeding female was absent. This would decrease the number of male helpers in the long-term because helper males that dispersed or died would not be replaced. We have noticed delays of two to three years for single male clusters to obtain a breeding female in the ANF. A lag period would occur between the time forest removal occurred and a reduction in woodpecker group size was observed. Breeding pairs may live four to five years or longer before one of the pair dies. If the breeding female dies, or the breeding male dies and is replaced by a male offspring, the cluster must be found by a dispersing female (see Walters et al. 1988). Our test of this fragmentation-dispersal hypothesis using a comparison of single male clusters with breeding pair clusters suggests that dispersal was not a problem. Although habitat around clusters with single males had greater habitat loss than clusters with only breeding pairs, the differences were not significant (Table 5).

Most forest removal that has occurred in the areas where our small populations exist (ANF, DCNF, and eastern portion of the SHNF) has occurred within the past four to 20 years. These areas also have extensive and numerous patches of private (non federal) holdings within the outside boundaries of the National Forests that are largely agricultural or other nonforest areas. In contrast, the portion of the Raven Ranger District where the large, dense population exists has few private holdings within it. Also, most loss of forest habitat in the Raven Ranger District occurred around active clusters 3–5 years prior to our study as a result of a major

southern pine beetle (*Dendroctonus frontalis*) epidemic from 1983 to 1985 (Billings and Varner 1986). Although the Raven population has twice as many active clusters around each active cluster than the small populations, it also has had about 15% more forest habitat loss than the small populations (Table 4). If too short a time period has passed to detect an effect of habitat loss on the dense Red-cockaded Woodpecker population in the Raven Ranger District, our results suggest that there may be a major reduction in group size in this population over the next 10 years.

It may be possible to have sufficient foraging habitat within 800 m of an active cluster, and still have insufficient foraging habitat for a woodpecker group because of forest fragmentation. Fragmentation that affects a woodpecker group's access to foraging habitat by forcing access routes to go through the territories of adjacent woodpecker groups may increase the probability of cluster inactivation.

Habitat loss appears to affect woodpecker group size by causing both dispersal and foraging sufficiency problems. It remains difficult to distinguish which mechanism has the greater effect.

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CAVITY TREE SELECTION BY RED-COCKADED WOODPECKERS IN RELATION TO TREE AGE

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Abstract.—We aged over 1350 Red-cockaded Woodpecker (*Picoides borealis*) cavity trees and a comparable number of randomly selected trees. Resulting data strongly support the hypothesis that Red-cockaded Woodpeckers preferentially select older trees. Ages of recently initiated cavity trees in the Texas study areas generally were similar to those of cavity trees initiated during the last several decades. In effect, the birds are continuing to select the oldest trees from a pool of trees of increasing age. This suggests that the current average age of cavity trees on these sites (85–130 yrs) may not provide optimum cavity trees for this endangered species. *Received 15 July 1990, accepted 27 March 1991.*

The Red-cockaded Woodpecker (*Picoides borealis*) is an endangered species endemic to pine forests of the southeastern U.S. (Jackson 1971). Deforestation and alteration of remaining forest habitat have severely affected Red-cockaded Woodpecker populations; current populations are isolated, and most are declining (Jackson 1971, Lennartz et al. 1983, Conner and Rudolph 1989, Costa and Escano 1989).

It has been generally accepted that Red-cockaded Woodpeckers select older pines for cavity excavation (e.g., Jackson 1971, Jackson et al. 1979, Locke 1980). Average ages of Red-cockaded Woodpecker cavity trees range from 62–149 years (Lennartz et. al. 1983, Hovis and Labisky 1985, Conner and O'Halloran 1987, DeLotelle and Epting 1988, Hooper 1988).

Several hypotheses have been suggested to account for the selection of older pines as cavity trees by Red-cockaded Woodpeckers (Beckett 1971, Conner and Locke 1982, Jackson and Jackson 1986). Red heart fungus (*Phellinus pini*) decays the heartwood of living pines and facilitates the excavation of cavities by Red-cockaded Woodpeckers (Jackson 1977a, Conner and Locke 1982). *P. pini* incidence increases with tree age, and southern pine species younger than 60 years are rarely infected (Nelson 1931; Wahlenberg 1946, 1960; Hepting 1971). Consequently, the hypothesis that Red-cockaded Woodpeckers select older trees with red heart decay, or at least an increased probability of decay, has received considerable support.

An additional series of hypotheses relate to the correlation between tree age and size. Older and larger trees allow cavities to be placed at greater

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heights. The presence of sufficient heartwood and red heart decay at greater heights are the primary controlling factors. Cavities at greater heights may experience less predation (Jackson 1974, Conner and O'Halloran 1987), less fire damage due to igniting of resin (Conner and Locke 1979), and less girdling of trees at cavity due to woodpecker excavations (Jackson 1985). The decreasing availability of suitable old trees has been hypothesized as a major contributing factor in the decline of the species (Steirly 1957, Ligon 1970, Jackson 1971, Jackson et al. 1979, Lennartz et al. 1983).

In a recent comment, Field and Williams (1985) focused attention on the limited data supporting the conclusion that old pines are a critical feature of Red-cockaded Woodpecker habitat. Field and Williams were able to locate only seven studies that provided data on the ages of cavity trees and potentially available trees. Several of these studies, because they were not specifically designed to address the question of cavity tree age, are of limited applicability. Subsequent studies (Hovis and Labisky 1985, Conner and O'Halloran 1987, DeLotelle and Epting 1988, Hooper 1988) have substantially rectified this situation.

Although the use of older relict trees by Red-cockaded Woodpeckers is now well established, the issue of preferred age has not been investigated previously. Most forests currently occupied by Red-cockaded Woodpeckers are relatively young (<150 yrs) with a low frequency of older relict trees. We hypothesize that although Red-cockaded Woodpeckers currently select cavity trees from among the oldest trees available, the age distribution available is not sufficient to provide potential cavity trees of the preferred ages. Three scenarios exist for the selection of older cavity trees by Red-cockaded Woodpeckers: (1) a threshold tree age exists beyond which the birds are not selective, (2) an optimum tree age exists, and (3) the birds select the oldest trees available.

During the course of extensive Red-cockaded Woodpecker surveys on U.S. Forest Service land in Texas, we collected extensive data on ages of Red-cockaded Woodpecker cavity trees. We also collected age data on non-cavity trees for comparative purposes. These data provide additional insight into the selection of potential cavity trees by Red-cockaded Woodpeckers and allow a partial test of the above hypothesis.

STUDY AREAS AND METHODS

The study was conducted on the Angelina (62,423 ha), Davy Crockett (65,359 ha), and Sam Houston (65,218 ha) National Forests located in eastern Texas. The Davy Crockett (DCNF), Sam Houston (SHNF) and northern portion of the Angelina (ANF) National Forests are comprised of pine and mixed pine-hardwood stands on the uplands and mixed hardwood stands on the bottomlands. Loblolly pine (*Pinus taeda*) and shortleaf pine (*P. echinata*)

predominate, and longleaf pine (*P. palustris*) is extremely rare. The southern portion of the ANF is similar except that the dominant pine is longleaf, and upland hardwoods are less frequent. Detailed descriptions of the ANF and DCNF study areas can be found in Conner and Rudolph (1989).

Recent surveys (Rudolph and Conner 1988, Conner and Rudolph 1989) provide Red-cockaded Woodpecker population data for these forests. The ANF and DCNF each support fewer than 30 active clusters (colonies in past literature, see Walters et al. 1988), and are declining. The SHNF supports 130+ active clusters, and the current population trend is unknown. In addition, numerous inactive clusters are present on each forest.

Location data for all known Red-cockaded Woodpecker clusters on Texas National Forests were obtained from the Forest Supervisor's office in Lufkin, Texas. We visited cluster sites on the DCNF and SHNF during 1987–1988. Cluster sites on the ANF were visited between 1983 and 1988.

Cavity trees were located and a 5-mm diameter increment core was extracted from each tree at breast height. A binocular dissecting scope was used to count annual growth rings. A correction factor (three years for loblolly and shortleaf, five years for longleaf) was added to each core count to allow for initial growth to breast height. Pine species, cavity tree status (active or inactive) (Jackson 1977b, 1978), and number of cavities and cavity starts were recorded for each tree.

Examination of cavity trees and existing records indicated that most have been cavity trees for several to many years. However, a subset of cavity trees was judged to have been initiated recently as cavity trees based on four criteria: (1) currently active, (2) lack of a developed plate around cavity entrance (Jackson and Jackson 1986), (3) lack of an extensive resin well system, and (4) lack of additional cavities not meeting these criteria. Although a specific length of time since these trees were first initiated as cavity trees cannot be established, as a group they should represent the most recently established cavity trees in these populations. Sequential observations, especially on the ANF, indicate that once cavity excavation is complete most trees fail to meet the above criteria within 1–2 years.

Data were collected from non-cavity trees in areas adjacent to Red-cockaded Woodpecker clusters. A mature timber stand between 150 m and 750 m from each cluster was chosen based on overall similarity to cluster stands. Availability of suitable stands determined the degree of similarity. Trees within these stands were randomly selected (N = number of cavity trees in adjacent clusters) by rotating a spinning device and selecting the nearest tree in the direction indicated. Differences in final sample size (Table 1) were due to slight variation in species composition and number of cores unusable due to decay. Random trees were chosen subject to a size restriction (≥30 cm DBH) and inclusion in the canopy, criteria that cavity trees rarely violate.

Data were also collected from a sample of non-cavity trees within stands containing clusters using the same methods as for random trees. Clusters sampled were on the DCNF (loblolly and shortleaf) and ANF (longleaf). Clusters containing ≥eight cavity trees and one or more recently initiated cavity trees were selected for sampling of non-cavity trees.

RESULTS

Data were obtained on 1368 cavity trees and 1355 random trees (exclusive of random non-cavity trees within clusters). Mean ages (years) of cavity trees were 131.1 for longleaf pine, 90.0 for loblolly pine, and 104.2 for shortleaf pine. Significant differences were detected between mean ages of all three species of cavity trees (ANOVA, $P < 0.001$; Duncan's Multiple Range test, $P < 0.05$).

Mean ages of cavity trees were significantly greater (18.7–68.2 years)

TABLE 1
AGE OF RED-COCKADED WOODPECKER CAVITY TREES AND RANDOM TREES (150–750 M) FROM CLUSTERS ON THREE NATIONAL FORESTS IN TEXAS

Forest	Species	Type	N	Mean	Range	SD	P^a
Angelina	*Pinus palustris*	Cavity	149	130.0	49–332	45.5	
		Random	157	61.8	38–169	21.7	<0.001
	P. taeda	Cavity	45	87.0	52-112	16.1	
		Random	50	66.8	28–107	16.9	<0.001
	P. echinata	Cavity	20	100.5	86–132	11.1	
		Random	28	70.8	44–110	16.4	<0.001
Davy Crockett	*P. taeda*	Cavity	151	96.5	66–156	13.1	
		Random	97	70.8	35–111	18.1	<0.001
	P. echinata	Cavity	190	105.1	63–169	16.6	
		Random	170	85.6	51–165	19.1	<0.001
Sam Houston	*P. taeda*	Cavity	728	88.7	49–133	14.2	
		Random	658	70.0	32–123	14.7	<0.001
	P. echinata	Cavity	85	103.4	54–125	14.8	
		Random	195	82.9	51–124	18.1	<0.001

[a] One-tailed *t*-test.

than those of random trees distant from clusters in all cases, regardless of tree species or National Forest (Table 1).

In 11 of 14 cases, cavity trees were significantly older than non-cavity trees within the same stand (Table 2). Mean ages of cavity trees ranged from 2.6–33.9 years older than random trees within these stands. The three exceptions involved shortleaf pine in stands containing few younger trees. These combined data were also analyzed by means of one-way and two-way ANOVA. Significant differences were found between cavity tree ages and non-cavity tree ages ($P < 0.001$), indicating that the differences transcend tree species and stands.

A total of 140 cavity trees were identified as recently initiated by the criteria listed above. The ages of these trees were compared to those of all other cavity trees. In five of the seven cases, there was no significant difference between the mean age of recently initiated cavity trees and all other cavity trees (Table 3). The two significant comparisons involved loblolly pine on the DCNF and SHNF. Mean ages of recently initiated cavity trees were 13.5 and 6.2 years younger, respectively, than all other cavity trees in these two significant cases ($P < 0.001$).

DISCUSSION

Our results indicate clearly that Red-cockaded Woodpeckers select older pines for cavity excavation. This preference is maintained for each of the three pine species used in Texas and on three different national forests.

TABLE 2

AGE OF RED-COCKADED WOODPECKER CAVITY TREES AND NON-CAVITY TREES WITHIN STANDS ON THREE NATIONAL FORESTS IN TEXAS

Species	Cluster	Type	N	Mean	Range	SD	P^a
Pinus palustris	3	Cavity	10	110.2	83–175	28.7	
		Non-cavity	10	76.3	48–98	18.5	<0.01
	4	Cavity	9	95.1	80–105	7.3	
		Non-cavity	10	78.7	44–100	23.3	<0.05
	5	Cavity	6	109.8	81–148	26.4	
		Non-cavity	20	84.7	76–95	5.6	<0.05
	6	Cavity	6	97.3	86–103	6.5	
		Non-cavity	10	87.2	61–101	11.1	<0.05
	7	Cavity	8	104.6	89–126	13.2	
		Non-cavity	10	89.2	71–106	11.8	<0.01
	8	Cavity	6	111.8	100–149	18.5	
		Non-cavity	15	93.0	80–102	5.7	<0.05
P. taeda	1	Cavity	5	86.8	69–107	17.1	
		Non-cavity	5	69.2	49–76	11.3	<0.05
	2	Cavity	6	99.2	96–103	3.1	
		Non-cavity	9	75.6	68–86	5.4	<0.001
	9	Cavity	3	111.3	110–113	1.5	
		Non-cavity	8	95.0	74–106	11.3	<0.01
P. echinata	2	Cavity	7	106.3	74–154	25.4	
		Non-cavity	11	73.2	60–80	5.9	<0.001
	9	Cavity	5	98.4	91–111	8.4	
		Non-cavity	10	99.7	88–112	7.1	N.S.
	10	Cavity	5	104.6	98–113	5.6	
		Non-cavity	10	99.2	87–110	6.6	N.S.
	11	Cavity	4	108.3	104–113	4.0	
		Non-cavity	10	99.6	91–108	5.4	<0.01
	12	Cavity	13	118.6	107–130	7.2	
		Non-cavity	10	116.0	108–122	4.9	N.S.

[a] One-tailed *t*-test.

This result is consistent with previously published studies (Lennartz et al. 1983, Hovis and Labisky 1985, Conner and O'Halloran 1987, DeLotelle and Epting 1988, Hooper 1988).

Even within stands the selection of older pines is also apparent. That the age of cavity trees was significantly greater than that of non-cavity trees within stands suggests that selection is based on individual trees and not on selection of older stands. The three exceptions were situations that provided minimal opportunity for selection based on age. The average ages of trees in these stands (99.2–116 years) included three of the four oldest averages among stands examined, and the ranges of tree ages were

TABLE 3
AGE OF RECENTLY INITIATED AND ALL OTHER RED-COCKADED WOODPECKER CAVITY TREES ON THREE NATIONAL FORESTS IN TEXAS

Forest	Species	Type	N	Mean	Range	SD	P^a
Angelina	*Pinus palustris*	all other	136	130.8	49–332	46.2	
		recently initiated	13	122.2	80–200	37.8	N.S.
	P. taeda	all other	42	87.7	52–112	16.0	
		recently initiated	3	76.7	62–97	18.2	N.S.
	P. echinata	all other	19	100.7	86–132	11.4	
		recently initiated	1	96.0	96	0.0	N.S.
Davy Crockett	*P. taeda*	all other	137	97.7	66–156	12.5	
		recently initiated	16	84.2	69–108	12.3	<0.001
	P. echinata	all other	158	105.0	63–169	16.6	
		recently initiated	30	105.7	74–161	17.2	N.S.
Sam Houston	*P. taeda*	all other	652	89.3	49–133	14.0	
		recently initiated	68	83.1	59–120	15.1	<0.001
	P. echinata	all other	72	104.6	64–125	12.7	
		recently initiated	9	98.1	59–120	21.2	N.S.

[a] One-tailed *t*-test.

narrow. A similar pattern has been reported by DeLotelle and Epting (1988).

Cavity tree selection by Red-cockaded Woodpeckers is a complex process. Tree diameter, presence of redheart fungus, heartwood diameter, bole length, growth history, and resin characteristics have all been demonstrated to vary between cavity trees and non-cavity trees (Jackson 1977a, Jackson et al. 1979, Conner and Locke 1982, Hovis and Labisky 1985, Conner and O'Halloran 1987, Hooper 1988). In addition, stand characteristics, including basal area, midstory development, and canopy height, have been demonstrated to vary between cluster stands and non-cluster stands (Hooper 1988, Locke et al. 1983, Hovis and Labisky 1985, Conner and O'Halloran 1987, Conner and Rudolph 1989). Correlations between these variables and tree age are common. Consequently, a multiplicity of factors is available as a basis for cavity tree selection by Red-cockaded Woodpeckers. Conner and O'Halloran (1987) have presented evidence suggesting that individual tree characteristics are more important than stand characteristics. The specific criteria used by Red-cockaded Woodpeckers in choosing cavity trees are unknown. However, the ultimate result, that older trees are selected, is well documented.

Questions relating to the preferred age of cavity trees are more difficult

to answer. Our data, analyzed by forest and by species, indicate that in most cases there is no significant difference between mean ages of recently initiated cavity trees and all other cavity trees. Jackson et. al. (1979) and Hovis and Labisky (1985) have previously reported average ages for recently initiated cavity or start trees (variously defined). Although average ages were not compared to other cavity trees statistically, their data suggest that average ages of recently initiated trees are similar to those of all cavity trees.

Engstrom and Evans (1990) have recently presented data suggesting that even in an old growth longleaf pine stand, Red-cockaded Woodpeckers are selecting the older trees from among those available. Two additional data sets also indicate use of very old trees. Teitelbaum and Smith (1985) reported estimated cavity tree ages in excess of 150 years for loblolly pine and 300 years for longleaf pine, based on an age-diameter relationship determined for non-cavity trees. We recently confirmed these ages by coring the actual cavity trees. Hedrick (unpubl. data) reports a mean age of 189 years for longleaf pine cavity trees in the Oakmulgee District of the Talledega National Forest. Maximum age was 368 years for an active cavity tree.

Our conclusion from this pattern is that as the regenerating forests in Texas continue to age from the initial logging 70–100 years ago (Maxwell and Baker 1983, Conner and O'Halloran 1987), Red-cockaded Woodpeckers are continuing to select cavity trees from the older available trees. The preferred age of cavity trees may be greater than the current age structure of the three forests provides. Consequently, the birds continue to select cavity trees from the older available trees with the result that the average of recently initiated cavity trees tracks the increasing age of the available trees. The data support our initial hypothesis that the tree age distribution available is not sufficient to provide potential cavity trees of the preferred ages. Our data also indicated that scenario (1), a threshold age beyond which the birds are not selective, is not operating. However, our data are not sufficient to differentiate between scenarios (2) and (3). This question can only be answered with data from older forests.

Significant age differences were detected between recently initiated cavity trees and all other cavity trees in the two cases of loblolly pines on the Davy Crockett and Sam Houston National Forests. This suggests that for this species, tree ages have advanced sufficiently to allow separation to develop between the age distributions of recently initiated cavity trees and all other cavity trees. That this has occurred in loblolly rather than shortleaf or longleaf pines is consistent with several characteristics of loblolly pine compared to other species. Loblolly pines are characterized by faster growth (Wahlenberg 1946), shorter lifespan (Platt et al. 1988),

and presence of more heart rot at younger ages (Nelson 1931; Wahlenberg 1960, pers. obs.) than the other species. Consequently, the optimum or suitable ages of loblolly pines for Red-cockaded Woodpecker cavity trees may be considerably younger than for the other pine species. Reported ages of cavity trees of the three species considered here are generally oldest for longleaf and shortleaf pine and youngest for loblolly pine (e.g., Wood 1975, Jackson et al. 1979, Jackson and Jackson 1986).

Several data sets now exist that support the hypothesis that Red-cockaded Woodpeckers select old pines as cavity trees. The existence of a threshold age of 60–80 years is also indicated by these data sets (DeLotelle and Epting 1988, Hooper 1988). The incidence of cavity trees of younger age is rare. Tree species, availability of older trees, incidence of heart rot, etc. influence the average age of cavity trees but do not greatly affect the minimum age.

Above the threshold age, the suitability of pines as potential cavity trees presumably increases. This increase is suggested by several of the data sets and is strongly supported by the data presented above. However, these data only apply to a limited age span above the threshold age due to the current rarity of pine stands of advanced age (i.e., those with significant numbers of trees in excess of 100 years). The shape of a suitability curve may plateau, peak, or continue to increase with increasing tree age. Current data are insufficient to distinguish among these alternatives.

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THE RELATIONSHIP BETWEEN BREEDING BIRD DENSITY AND VEGETATION VOLUME

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Abstract.—An index of total vegetation volume was strongly correlated with breeding bird density at 31 sites in four separate studies conducted in southwestern shrub and desert habitats between 1974 and 1987. Vegetation volume was not as strongly correlated with winter bird density in two of these studies. We suggest that these correlations indicate that breeding birds respond strongly to resources associated with vegetation and that such a resource-based response may explain such well-known patterns as the edge effect and the high avian breeding densities in southwest riparian habitats. The technique we describe for measuring total vegetation volume provides a quick and accurate method of estimating this simple aspect of vegetation structure and may be useful in describing plant communities quantitatively. *Received 26 Feb. 1990, accepted 29 May 1991.*

An underlying assumption of theoretical models of avian community structure generated in the 1960s is that the number and diversity of birds in an area reflect the availability of critical resources. This linkage between community structure and resources was supported initially by MacArthur and MacArthur's (1961) demonstration of a close correlation between foliage diversity (FHD) and bird species diversity (BSD). Since then the relationship between vegetation structure and avian community parameters has been the subject of much research. Although widely accepted at first, the BSD/FHD relationship and, by association, the underlying resource assumption have come under strong criticism for two reasons. First, while some studies confirmed the empirical relationship described by MacArthur and MacArthur (MacArthur et al. 1966, Karr and Roth 1971, Terborgh 1977, Moss 1978, Dickson and Segelquist 1979, Beedy 1981, Bell 1982), others did not (e.g., Stamp 1978, Conner et al. 1979, Karr 1980, Erdelen 1984, Engstrom et al. 1984). Thus, the generality of the proposed relationship appeared questionable. Secondly, both BSD and FHD were calculated using information indices, which hide important information by combining measures of species richness and relative abundance, and may lack a direct, biologically meaningful explanation (James and Rathbun 1981). Several authors have suggested that simpler population parameters with direct biological interpretation be used to quantify both vegetation and wildlife populations (Karr 1980, James and Rathbun 1981, Erdelen 1984). We propose that to assess properly the resource

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assumption that underlies MacArthur and MacArthur's original work, the relationship between vegetation characteristics and avian community patterns should be re-examined using these simple population parameters.

In this paper, we report the relationship between two such simple population parameters for avian communities in a variety of southwestern habitats. We first describe a simple method of measuring vegetation volume in habitats where vegetation is generally under 8 m in height. We then demonstrate that an index of vegetation volume generated by our measuring technique was closely correlated with total breeding bird density in four different studies. We suggest that these strong correlations provide evidence that breeding birds respond to critical resources as estimated by vegetation volume. This resource-based hypothesis may provide a biological explanation for several well-known patterns of avian distribution, including the edge effect and the high avian densities reported from desert riparian systems. Our study suggests that the assumption that community patterns reflect a dependence on critical resources is a viable hypothesis that deserves further examination.

METHODS

We first developed our technique for measuring vegetation volumes and documented the relationship between total vegetation volume (TVV) and breeding bird density (BBD) during a 1984 study of avian habitat selection in New Mexico. Because sample sizes in this study were small, we re-examined the TVV/BBD relationship by measuring vegetation volumes and bird densities at 15 sites in southern Arizona in 1985 and 1986. In this paper, we first present the results of this larger study to demonstrate the technique by which we measured vegetation volumes and to document the TVV/BBD relationship. We then briefly describe similar TVV/BBD correlations we found in three smaller data sets, including the original New Mexico study, to establish the generality of the relationship.

1985–1986 Arizona data.—We measured vegetation using a variation of the vertical-line intercept technique (MacArthur and Horn 1969). We refer to our variation of the technique as the "pole method." A 6-m pole was constructed from 18-mm diameter electrical conduit pipe and marked in decimeter and meter sections. We used this pole to measure an index of the volume of woody perennial plants in each meter layer above the ground. Holding the pole vertically at each point where TVV was to be measured, we counted the number of decimeter sections that contained vegetation within a radius of 1 dm from the pole. We therefore sampled a series of cylinders 0.1 m tall and 0.1 m in radius.

We called each decimeter cylinder that contained vegetation a "hit." The number of possible hits in each meter layer above the ground ranged from 0–10. We also recorded the species of plant that was responsible for each hit. If two or more plant species were present in the same meter layer, the total number of hits in that layer were allotted between the plant species according to the relative dominance of each plant within the layer. By holding the pole over our heads, we could count the number of hits in layers up to 8 m above ground. We estimated the number of hits in layers >8 m for the few plants reaching that height in the habitats we studied. Total vegetation volume (TVV) was estimated from these data as: $TVV = h/10p$; where h = the total number of hits summed over all meter layers at all points measured, and p = the number of points at which vegetation volumes were measured. TVV

has the units of cubic meters of vegetation per square meter, and in our study ranged from 0 to 2.0 for southwestern desert and shrub habitats. This technique overestimates actual vegetation volume because each decimeter cylinder containing any vegetation, regardless of amount, was counted as full. This error could be reduced by decreasing the radius or the height of the cylinder. Because of the manner in which data were collected, indices of vegetation volumes for each plant species and each meter layer could also be calculated, as well as indices of plant height, percent cover, and FHD.

We measured TVV and censused birds at 15 study sites located in the Tucson Valley, Pima County, Arizona in 1985 and 1986. All sites were located in the Arizona Upland Subdivision of the Sonoran Desertscrub or Riparian Deciduous Woodland and Scrubland biomes (Brown 1982) and reflected the natural distribution of vegetation types found in the Tucson Valley. TVV was measured as outlined above at 4–12 random plots selected at regular intervals along a transect through each major habitat. Specific plot locations were randomly chosen from starting points located at regular intervals along, and within 30 m of, transects used to census birds. A 20-m straight-line transect was established within each of the plots along a randomly determined heading from a point close to the center of each plot. Volume measurements were taken at 2-m intervals along this transect. A second 20-m transect was established perpendicular to the first, resulting in measurements from 20 points in each plot.

We compared the amount of variation in bird density explained by TVV with the amount of variation explained by other vegetation indices such as plant species diversity, FHD, and the vegetation volumes of particular plant species. FHD was calculated from the data collected by the pole method by treating each meter of the pole as a layer, and using the standard Shannon-Weiner information index $H' = -\Sigma\, p_i \ln p_i$, where p_i = the proportion of total hits found in the ith meter layer. The meters are not "layers" as traditionally thought of in FHD studies; that is, they are not necessarily separate levels of vegetation to which the birds may be responding (MacArthur and MacArthur 1961). However, the pole method allows FHD to be calculated using up to eight layers, which provides a more accurate profile of vegetation than usual measures of FHD.

We estimated bird densities using 0.6–4.6-km long variable-width belt transects (Emlen 1971). Areas censused ranged from 12–90 ha. We conducted winter bird censuses in December 1985 and January 1986 and breeding bird censuses in July 1986. All censuses were conducted between 05:00 and 09:00 h MST during suitable weather.

During the breeding season, densities for territorial birds were based on numbers of breeding pairs per 25 ha. A single adult bird of either sex, as well as two birds of opposite sexes together, was counted as a pair. Groups of birds composed of adults with recent fledglings were counted as one pair. Densities of non-territorial species, such as House Finches (*Carpodacus mexicanus*) or Brown-headed Cowbirds (*Molothrus ater*), were estimated from total counts, as were those of all birds in winter. Breeding density estimates were also based on total counts for species where young birds had dispersed and it was not possible to identify family groups (e.g., Cactus Wrens [*Campylorhynchus brunneicapillus*], Verdins [*Auriparus flaviceps*], and Gambel's Quail [*Callipepla gambelii*]). Birds flying over transects and the few migratory or visiting species encountered were not included in analyses.

New Mexico data set.—We also had access to vegetation volumes and bird densities from three smaller studies. Although most of these data were not collected specifically for examining the TVV/BBD relationship, we present them here to document the generality of the strong correlation between TVV and BBD in southwestern habitats. Techniques for measuring vegetation and bird densities differed among the studies; therefore, we cannot make strong comparisons among the different data sets. However, measurement techniques

were used consistently within each study. Thus, each study can be examined independently for evidence supporting the TVV/BBD relationship.

We measured vegetation volumes in six different biomes in Grant County, New Mexico, in March 1984 (Mills and Carothers 1986). Study sites were located in six habitat types: cottonwood-dominated Sonoran Riparian Deciduous Forest, box-elder dominated Sonoran Riparian Deciduous Forest, mesquite-dominated Sonoran Riparian Deciduous Woodland, Madrean Evergreen Woodland, Great Basin Conifer Woodland, and Semidesert Grassland (Brown 1982). Lists of dominant plants and birds recorded in this study and studies described below are available from the authors.

We measured volumes in 1–4 plots at each study site in a manner similar to that described above except for the following details. We estimated vegetation volumes within the cylinder described by a radius of 1 dm from each meter layer of a 5-m pole. The pole was not marked in decimeters, instead volume categories of 0.0, 0.1, 0.5 and 1.0 density were estimated for each meter layer. A value of 0.1 was given to any estimate of volume ≤0.1 of the total meter layer, 0.5 was given to any estimate between 0.1 and 0.5, and 1.0 was given to any estimate between 0.5 and 1.0. For vegetation taller than could be recorded by the 5-m pole, a single estimate of the volume in all remaining layers was made.

For a number of plots, vegetation volumes were measured by both the pole method and the shapes and plots method (Balda 1969). The shapes and plots method is an alternate technique for measuring volumes in which plants are classified into general geometric shapes, and volumes are estimated from appropriate height and width measurements. To correct for variation in density within plants, we visually assigned each plant into density classes of 0.1, 0.5, or 1.0, which was then multiplied by the total volume. We censused birds in New Mexico along 2–4 km long variable-width belt transects as described above. Areas of study sites ranged from 40–80 ha. For small, well-defined, long and narrow, or irregularly shaped habitats, such as riparian forests, we estimated total bird densities based on total counts of birds and areas measured from aerial photographs with a planimeter. Breeding bird censuses in these habitats were conducted in June and July 1983, while winter censuses were conducted in January and February 1983.

1987 Arizona data.—We measured vegetation volumes and censused birds at six Sonoran Desertscrub or Riparian Deciduous Woodland sites in the Tucson Valley, Pima County, Arizona, from April through July, 1987. These sites served as native-vegetation control sites for a larger study of the relationship between vegetation volume and the densities of urban birds. Two of the six control sites had been used in the 1985–1986 Arizona study. Vegetation volumes were measured as in the 1985–1986 Arizona study. We measured vegetation volumes and recorded plant species at 10 plots per study site in May–July 1987. We censused birds using fixed-width belt transects (Emlen 1971). All transects were 800 m (½ mi) long and 49 m (160 ft) wide. This produced a total census area of 3.9 ha (10 acres) at each site. The size of the plots was dictated by limitations on plot size in the urban areas for which these plots served as controls.

All bird censuses were conducted in April and May 1987 between 05:00 and 09:00 h MST. Fledglings, visitors, and migrants were not included in density estimates. Because non-territorial birds such as doves and House Finches could be using the sites in a manner different than territorial birds (Anderson et al. 1983), we calculated the relationship between TVV and total bird density both with and without these species in this data set.

Verde River, Arizona, data.—Carothers et al. (1974) provide vegetation volumes and bird censuses for four cottonwood-dominated Sonoran Riparian Deciduous Forests along the Verde River in central Arizona. They estimated vegetation volumes with the shapes and plots method without any correction for internal foliage volume. For our analysis, we

eliminated from total bird densities both European Starlings (*Sturnus vulgaris*), which apparently used these sites only for roosts, and all bird species directly dependent on water.

Statistical analysis.—We used simple linear regression to examine the relationship between TVV and total bird density, calculating correlation coefficients (r) and examining residuals to determine the strength of the correlations. To correct for departures from normality, we applied a square-root transformation to the vegetation volume data, and a $\log_{10}$ transformation to the density, species richness, and FHD data. Although we ran all statistical tests on the transformed data, we present the untransformed data in Fig. 1 for clarity. Significance of regression coefficients was accepted at the $P < 0.05$ level for all statistical tests.

We also ran a series of simple linear regressions using bird density as the dependent variable and a number of vegetation characteristics as the independent variables. These tests were done to determine if TVV explained more variance in bird density than did FHD, plant species richness, or the volumes of the most common plant species. When a series of statistical tests are examined simultaneously in this manner, there exists a high probability of Type I error (incorrectly rejecting a true null hypothesis) (Rice 1989). Accordingly, we performed a sequential Bonferroni test to determine if all r values with $P < 0.05$ should be considered significant. Four of the seven regressions in this series yielded r values with $P < 0.05$, and all four of these results should be considered significant at a table-wide significance level of $P = 0.05$, according to the Bonferroni procedure. Finally, we also used stepwise multiple regression to see if TVV or other vegetation parameters were consistently loaded first into a regression model explaining density variance.

RESULTS

1985–1986 Arizona data.—Total vegetation volume (TVV) and total breeding bird density (BBD) for the 15 sites in southeastern Arizona were highly correlated ($r = 0.930$, $P = 0.0001$, Fig. 1). Examination of the residuals showed an extremely close fit to the linear model. TVV and wintering bird density were not significantly correlated at the eight sites where winter censuses were conducted ($r = 0.485$, $P = 0.223$). However, TVV was significantly correlated ($r = 0.787$, $P = 0.020$) with the winter density of bird species that are not primarily seedeaters (sparrows, finches, and quail).

TVV was always the first variable loaded into the stepwise multiple regression models that related variation in BBD to seven vegetation structure and floristics variables. TVV had a higher r value ($r = 0.93$) in these regression models than did FHD ($r = 0.865$, $P = 0.0001$), plant species richness ($r = 0.437$, $P = 0.103$), and the volumes of the four most widespread plant species (*Prosopis juliflora,* $r = 0.789$, $P = 0.0005$; *Larrea tridentata,* $r = -0.378$, $P = 0.164$; *Acacia constricta,* $r = 0.007$, $P = 0.979$; *Acacia greggii,* $r = 0.746$, $P = 0.0014$).

Other data.—TVV and BBD for the six New Mexico sites were also highly correlated ($r = 0.951$, $P = 0.0036$; regression equation for transformed variables: $y = 0.58x + 1.91$). Examination of the standardized residuals showed no significant departure from a normal distribution

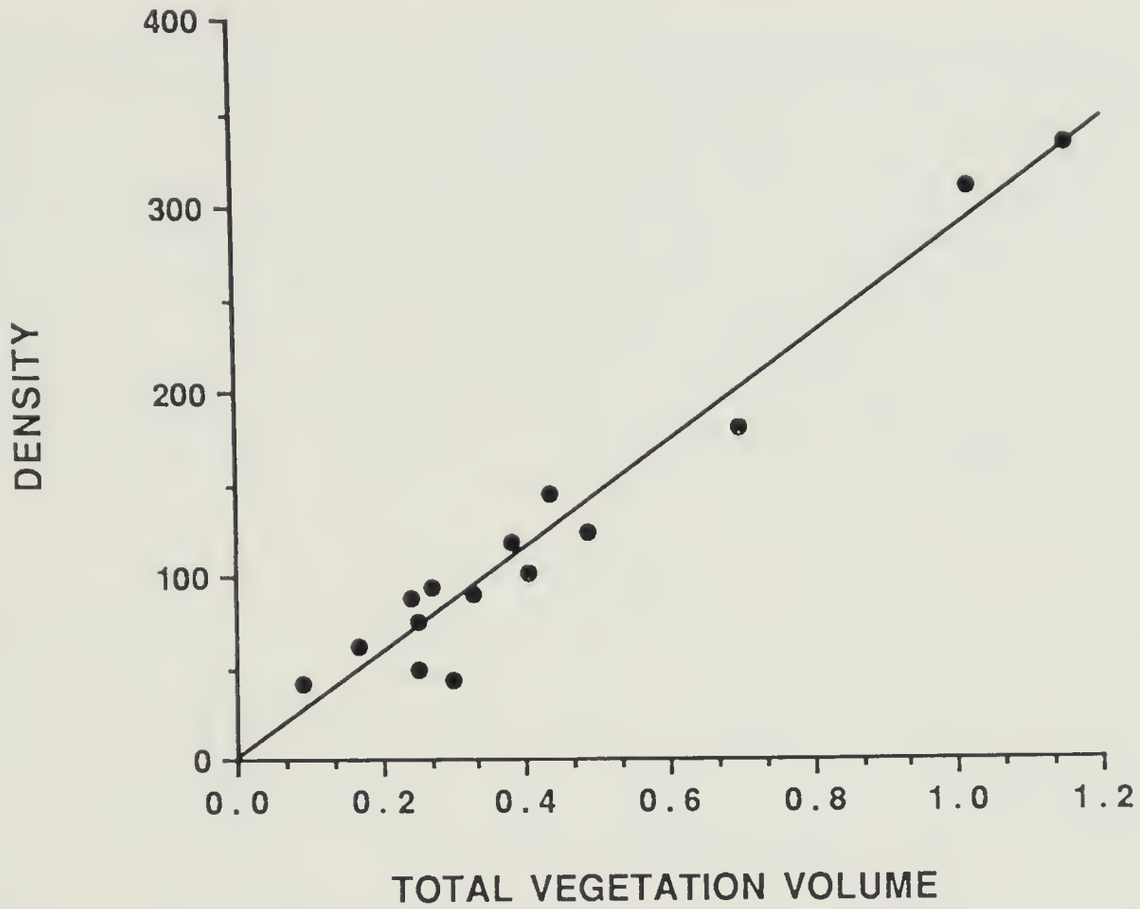

FIG. 1. Total breeding bird density (pairs per 25 ha) as a function of total vegetation volume (TVV) for the 1985–1986 Arizona study sites. Regression equation: y = 290x − 1.0.

(Kolmogorov-Smirnov test for goodness of fit, $P > 0.05$); however, sample sizes were very small. Inspection of the residuals suggested a curvilinear function might fit the data better than the linear model, but with only six data points no strong conclusion can be made. For the five study sites censused in winter, TVV was not significantly correlated with total wintering bird density ($r = 0.824$, $P = 0.086$) or with non-seedeaters ($r = 0.818$, $P = 0.090$).

Values of vegetation volumes generated with the pole method and shapes and plots method were highly correlated ($r = 0.979$, $P = 0.004$, $N = 5$). Volume estimates derived from the shapes and plots method were higher than those from the pole method (about 1.9 times higher for the four lowest points; Mills, unpubl. data).

In the 1987 Arizona data set, a significant correlation was found between TVV and BBD at the six control sites ($r = 0.866$, $P = 0.026$, regression equation: y = 0.30x + 1.37). The regression did not change substantially when non-territorial and exotic species were removed from the density data ($r = 0.873$, $P = 0.023$). In the 1987 data set, FHD correlated better with BBD than did TVV (FHD: $r = 0.947$, $P < 0.0041$). However, the

densities of non-territorial native birds (doves and finches) and the non-native House Sparrow (*Passer domesticus*) were increased at some of our 1987 Arizona sites that were close to urban areas, and we suspect that this increase masked the TVV/BBD relationship. When non-territorial birds and exotic species were removed from the density data, TVV loaded as the first variable into the stepwise regression model. None of the sites in the other studies was close to urban areas.

Finally, there was a significant correlation between TVV and BBD at the four cottonwood forest sites described by Carothers et al. (1974) (r = 0.999, P = 0.0008; regression equation: y = 0.005x + 3.51).

DISCUSSION

Significant correlations were found between TVV and BBD in all four studies. This result appears quite robust, since the regressions were uniformly high in spite of wide variation in the habitats sampled and variations in the methods of measuring bird density and vegetation volume. Although the habitats sampled in both of the Arizona studies were mostly from within the same biome, few dominant plant or bird species were shared between study sites. Even fewer shared species were recorded between sites in the New Mexico study because sites were mostly from different biomes. Although vegetation volume estimates were based on small sample sizes in the New Mexico study, the correlation between TVV and BBD was still high. The relationship between vegetation volume and bird density appeared to exist both within the same plant community and between different types. This suggests that, within the range of southwestern habitats we sampled, breeding bird density correlated with vegetation volume regardless of plant species composition. Additional studies from other shrubby habitats are necessary to test the generality of this empirical relationship.

Other studies that examined correlates of bird density have found that foliage volume accounted for a significant portion of the variation in bird density or species richness (Anderson et al. 1983, Meents et al. 1983, Robinson and Holmes 1984, Vander Wall and MacMahon 1984, Verner and Larson 1989). Some workers have found that other vegetation parameters such as percent foliage cover and FHD correlate significantly with bird density (Shurcliff 1980, Hino 1985); in general, these studies did not measure vegetation volume.

A number of studies suggest that measures of floristics such as densities of individual plant species are more important determinants of bird community parameters than are physiognomic (structural) measures (Kroodsma 1982; Rice et al. 1983, 1984; Rotenberry 1985). Findings of these

studies do not conflict with the TVV/BBD relationship we describe. Many of these studies used presence/absence data of individual bird species, while we examined variation in total bird density. Even though some studies include bird densities and indices of vegetation volume in their data sets (i.e., Rotenberry 1985), analyses are usually based on similarity indices, which compare proportions of various parameters and do not include total bird densities or total vegetation volume.

These studies also emphasize that individual bird species are often closely associated with individual plant species. Many such relationships are well-known (e.g., Meents et al. 1982), and some were apparent in our data sets. Floristics and physiognomy are both important in determining avian community structure. With individual bird species responding in different ways to floristics and physiognomy, the strong correlation between total vegetation volume and total breeding bird density is all the more remarkable and has some interesting implications for community ecology. In particular, our results suggest that the total number of birds in southwestern lowland habitats is dependent on some factor(s) associated with the amounts of vegetation present. If, as we argue below, these factors are the resources on which bird populations depend for successful breeding, then this would support the assumption underlying MacArthurian community ecology that resource levels determine consumer levels.

Resource-based hypothesis.—Simple indices lend themselves to biologically meaningful interpretation (Karr 1980, Erdelen 1984). A reasonable hypothesis for the strong correlations between vegetation volume and breeding bird density is that bird density is proportional to available resources. Vegetation volume is an accurate estimator of plant biomass (Fonteyn 1978, Schlesinger and Jones 1984); therefore, volume could be an accurate estimator of resources associated with plant biomass. If plants provide resources in proportion to their vegetation volume (by providing more insect prey, more nest sites, or more favorable daytime roosts, for instance), then bird density should be proportional to vegetation volume.

One line of evidence supporting the resource-based hypothesis comes from the lack of significant correlations between winter bird density and TVV as measured in the summer. A high percentage of wintering birds in the southwest are flocking granivores, which feed on grass and forb seeds gleaned from the soil or from weedy annual plants (Pulliam and Brand 1975). We would not predict these groups to be heavily dependent on the foliage of woody perennials, except perhaps for roost sites; thus, their numbers should not be correlated strongly with TVV. When these seedeaters are removed from the winter bird densities, a significant cor-

relation occurred between TVV and winter bird density in the 1985–1986 Arizona data set but not the New Mexico data set.

Areas of high foliage volumes are often recognized as sites of high breeding bird densities. Riparian habitats of the southwest have long been recognized as supporting among the highest bird densities in North America (Carothers and Johnson 1975). It appears likely that high vegetation volume and the associated resource levels can account for these high bird densities. In our samples, cottonwood riparian forest had the highest TVV values we recorded.

Another well-known pattern that may be explained by vegetation volume is the edge effect, the increase in bird densities at the interface between habitat types. Many edge areas, especially where there is a large difference between habitats in canopy height, support high vegetation volumes because of the increased penetration of light to all foliage layers.

If the relationship between vegetation volume and bird density is resource-based, then fluctuations in resources should yield fluctuations in bird populations (Dunning and Brown 1982), and regions subject to disturbance should have more variable bird populations than areas with more stable resource levels. Dunning (1986) examined Breeding Bird Censuses and suggested that many North American habitats have relatively stable bird populations. We expect resources are relatively stable in these habitats and that vegetation volume might be a good estimator of bird density in these areas. Other habitats show wide density fluctuations attributable to disturbance of vegetation (e.g., flooding, Dunning 1986) and presumably, therefore, resource levels. We suggest that measurement of vegetation volume might be a useful tool in predicting changes in bird populations resulting from such disturbance-caused changes in resources. In areas where disturbance does not cause large-scale changes in vegetation, TVV will be of less use. Some shrub-steppe and grassland habitats might be examples of such areas, since Wiens (1974) proposed that bird populations in these habitats are strongly affected by unpredictable climatic instability during the breeding season.

In habitats dominated by exotic vegetation suspected to harbor low levels of insect prey (e.g., eucalyptus), bird densities are often lower than in apparently equivalent habitats dominated by native vegetation (Anderson et al. 1977). When exotic plants form a substantial proportion of an area's vegetation (such as in many urban areas), we expect lower correlations between TVV and BBD since vegetation volume will reflect available resources less accurately. In areas where these plants are native and contain significant insect faunas, we would expect higher correlations. In a simple test of these ideas, vegetation volumes were more correlated

with densities of native birds in urban neighborhoods landscaped mostly with native vegetation when compared to urban areas dominated by exotic plants (Mills et al. 1989).

We suggest that changes in vegetation volume should be considered when comparing bird communities within and between habitats. For instance, rarefaction has been suggested as a technique for standardizing species richness values within a habitat when study sites are of different sizes (James and Rathbun 1981). Rarefaction generates an expected number of species per number of individuals. Our study suggests that equal-area sites that differ widely in vegetation volume should support different numbers of individuals. Standardization of species richness values for both area effects (through rarefaction) and resource-level differences (as measured by vegetation volume) may be important for accurate comparisons between sites.

It may seem that our results merely restate the previously reported relationship between bird species diversity and foliage height diversity that has provoked such strong criticism. Our analyses are different, however. Our measure of vegetation, TVV, reflects the total amount of vegetation present in an area, not the distribution of vegetation within presumed "layers" of the environment, as does FHD. Similarly, breeding bird density is a simpler measure of avian community structure than is bird species diversity. The problems associated with diversity indices have prompted several authors (cited previously) to call for the use of simple measures of community structure. Using these simpler measures, we still find evidence consistent with the idea that the number of consumers in a community is determined by resource levels. Use of these simple community measures may allow more rigorous testing of the resource assumption than has been possible (Mills et al. 1989). We acknowledge that the data presented here do not constitute a test of the resource assumption. However, the present atmosphere in community ecology is such that we feel the value of examining resource-consumer relationships must be reestablished before specific tests of such relationships can be appreciated. Mills et al. (1989) present a simple test of the resource assumption using urban bird communities in Arizona.

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Wilson Bull., 103(3), 1991, pp. 480–485

SHORT COMMUNICATIONS

Observations of within-colony breeding synchrony in Jackass Penguins.—The Jackass Penguin (*Spheniscus demersus*) is a colonial seabird breeding year-round on the southern tip of the African continent. A west coast, winter breeding peak (May–September) has been found to occur, corresponding to peak food availability, lowered ambient temperatures, and maximum chick survival (Cooper 1980, Wilson 1985). At St. Croix Island on the east coast, it has been suggested that egg-laying peaks by Jackass Penguins show greater synchrony within colonies than over the island as a whole (Randall and Randall 1981). Synchrony of egg laying is believed to occur in breeding groups of Galapagos (*Spheniscus mendiculus*) (Boersma 1976) and crested (*Eudyptes*) penguins (Warham 1975). To date however, no data have been presented on the degree of synchrony between separate penguin colonies at a single breeding locality. This paper reports the occurrence of breeding synchrony in the Jackass Penguin at the colony level.

Methods.—We investigated breeding synchrony of Jackass Penguins nesting on Dassen Island (33°25′S, 18°16′E) situated off the west coast of South Africa. Between June and August 1989, we determined the date of brood initiation (hatching of first chick) for all nests in three low-density colonies. Low-density colonies were defined as areas accessible from the sea by a common landing point, and containing nests spaced 1–11 m apart. Birds within these areas are in sufficiently close proximity to experience regular social interactions. Daily checks of nests allowed us to determine the day of hatching (chick clear of the egg shell). The length of our field season prevented us from obtaining information on overall breeding success or dates of clutch initiation. We also counted nests in eight high-density colonies over one week in mid-July 1989. A high-density colony was defined as an aggregation of nests with inter-nest distances of approximately 1 m (Hockey and Hallinan 1981), with a minimum of 200 m separating adjacent colonies. Nests were typically shallow burrows within a common area of between 118 and 216 m^2. Inter-nest distances were measured as a straight line between nearest neighbors. Colony area was measured as a rectangle encompassing all measured nests. At each colony the contents of nests were categorized into one of three stages, each representing approximately six weeks of the offspring's dependent phase: (1) eggs (0–6 weeks; assuming all eggs are fertile), (2) downy chicks (6–12 weeks); and (3) down-droppers and fully feathered chicks (12–18 weeks), assuming a mean incubation period of six weeks (38 days, Williams and Cooper 1984), mean time from hatching to fledging 12 weeks (80 days, Williams and Cooper 1984), and a mean time from hatching until the development of true feathers six weeks (Table 1).

One of us (J.C.) counted numbers of active nests in eight distinct colonies at 10-day to one-month intervals during November 1971 to October 1972 at Dassen Island. Colonies

TABLE 1

LENGTH IN DAYS (MEAN ± SD, AND RANGE) OF THE BREEDING STAGES OF THE JACKASS PENGUIN

	Incubation	Hatch to down drop	Hatch to fledge
This study	—	44 ± 3 (40–50)	85 ± 9.2 (74–113)
Williams and Cooper (1984)	38 ± 0.8 (37–39)	—	80 ± 7.0 (65–90)

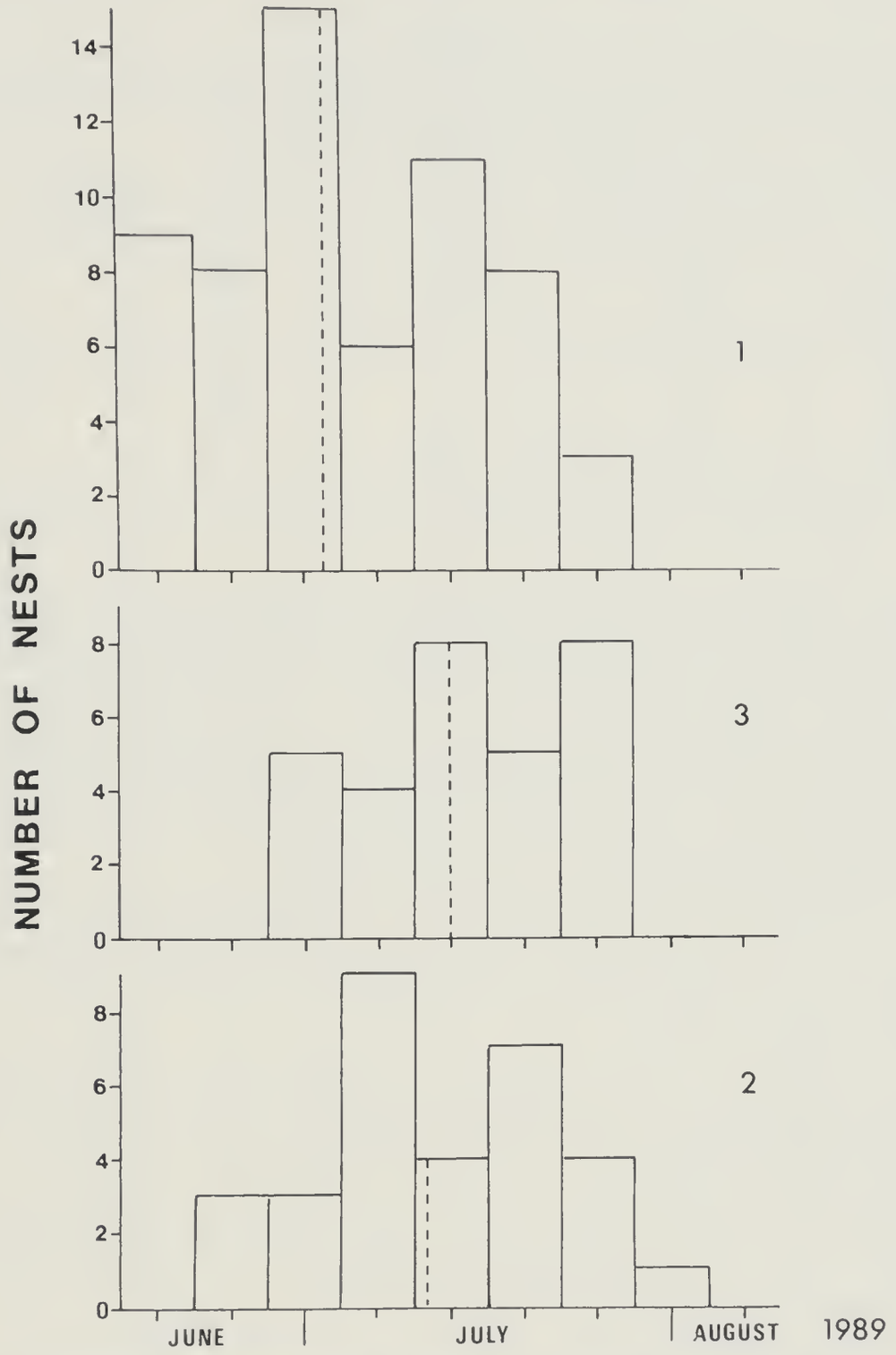


FIG. 1. Timing of chick-hatching in three low-density colonies of Jackass Penguins. Dotted lines indicate first 90% means.

were situated over the whole island, with no less than 100 m separating adjacent areas. At each visit the following were recorded: (1) the total number of active nest sites, i.e., nests containing eggs or chicks; (2) the number of nests containing a full clutch of two eggs; (3) the number of nests containing one or two small-downy chicks. Small-downy chicks were defined as chicks between one and 15 days old, and were characterized by their covering of sparse primary down. A census of active nests in discrete areas over a 12-month period allows the separation of localized breeding peaks from any general seasonal peaks.

Results.—There were peaks in the number of broods initiated in the three low-density colonies, with some clumping of hatching evident (Fig. 1). Means calculated from the first

Table 2

Ranges and Standard Deviations of Brood Initiation Dates in Three Low-density Jackass Penguin Colonies

Area	Number of nests	Span (days)					Standard deviation				
		First (%)			Mid (%)		First (%)			Mid (%)	
		100	90	50	90	50	100	90	50	90	50
1	62	39	33	17	33	19	10.3	9.1	5.5	9.0	5.3
2	32	40	30	19	28	14	9.6	8.3	5.8	8.0	5.1
3	30	26	23	12	23	14	8.0	7.1	3.9	7.2	4.4

90% of broods initiated show small between-colony differences suggestive of within-colony synchrony (Fig. 1). There was a significant difference in the timing of hatching between the three colonies (Kruskal-Wallis test statistic 18.02, df = 2, $P < 0.0001$). Hatching ranged over 26–40 days (Table 2). Similarities between first and mid-90% hatching ranges in all three areas indicate close intra-area mean and median values and, therefore approximately normal distributions (Table 2). However, differences between first and mid-50% spans of hatching in areas 1 and 3 suggest distributions skewed slightly to the left, and hence a tendency towards early egg laying (Table 2). First and mid-standard deviations indicate comparable degrees of synchrony in all three areas (Table 2).

Seven of the eight high-density colonies showed a significant bias in the proportions of stages represented (Table 3). The bias was not in a consistent direction between colonies; of the eight areas, four had mainly eggs, one had downy chicks, and down-droppers/feathered chicks predominated in three.

Proportions of nests containing two eggs in the eight colonies surveyed over 12 months show a seasonal peak around November, with a possible second peak between May and June. The precise placement of the two peaks differed between colonies (Fig. 2), ranging from early November to early January and from early June to late August. Some areas show a single peak seemingly independent of seasonal effects (e.g., area 4 peaks in early May). The occurrence of small downy chicks in nests reflects the two-egg peaks but shows more clearly the differences between areas with first peaks ranging from early November to late February and secondary peaks between May and August.

Discussion.—Although showing some clumping, hatching in low-density colonies was not highly synchronized. Variation within these colonies may have been due to sub-colony effects, with small denser aggregations of nests showing greater synchrony. Peaks in hatching were similar between the three low-density study colonies, and insufficient in themselves, due to the lack of data from earlier and later months, to distinguish between the passive synchronizing effect of a possible seasonal breeding peak and local-scale synchrony due to social stimulation.

Hailman (1964) examined synchrony in gulls by recording the proportions of birds at each breeding stage. This method allows a researcher to make approximate statements about synchrony based on brief visits and is satisfactory for comparisons among colonies of a single place or species (Gochfeld 1980). A synchronous colony would have most birds at one particular stage, while a less synchronous colony may have equal proportions at each stage. This type of census is particularly suited to Jackass Penguins, which may breed at any time during the year, so that any stage of breeding may be represented at any time.

TABLE 3
COUNTS OF BREEDING STAGES IN HIGH-DENSITY JACKASS PENGUIN COLONIES

Colony	Eggs	Downy young	Feathered young	Total
1	3	22	[24]	49**
2	16	10	[23]	49 NS
3	[14]	11	2	27*
4	8	13	[36]	57**
5	[30]	4	4	38**
6	[29]	7	3	39**
7	[31]	6	6	43**
8	5	[24]	5	34**

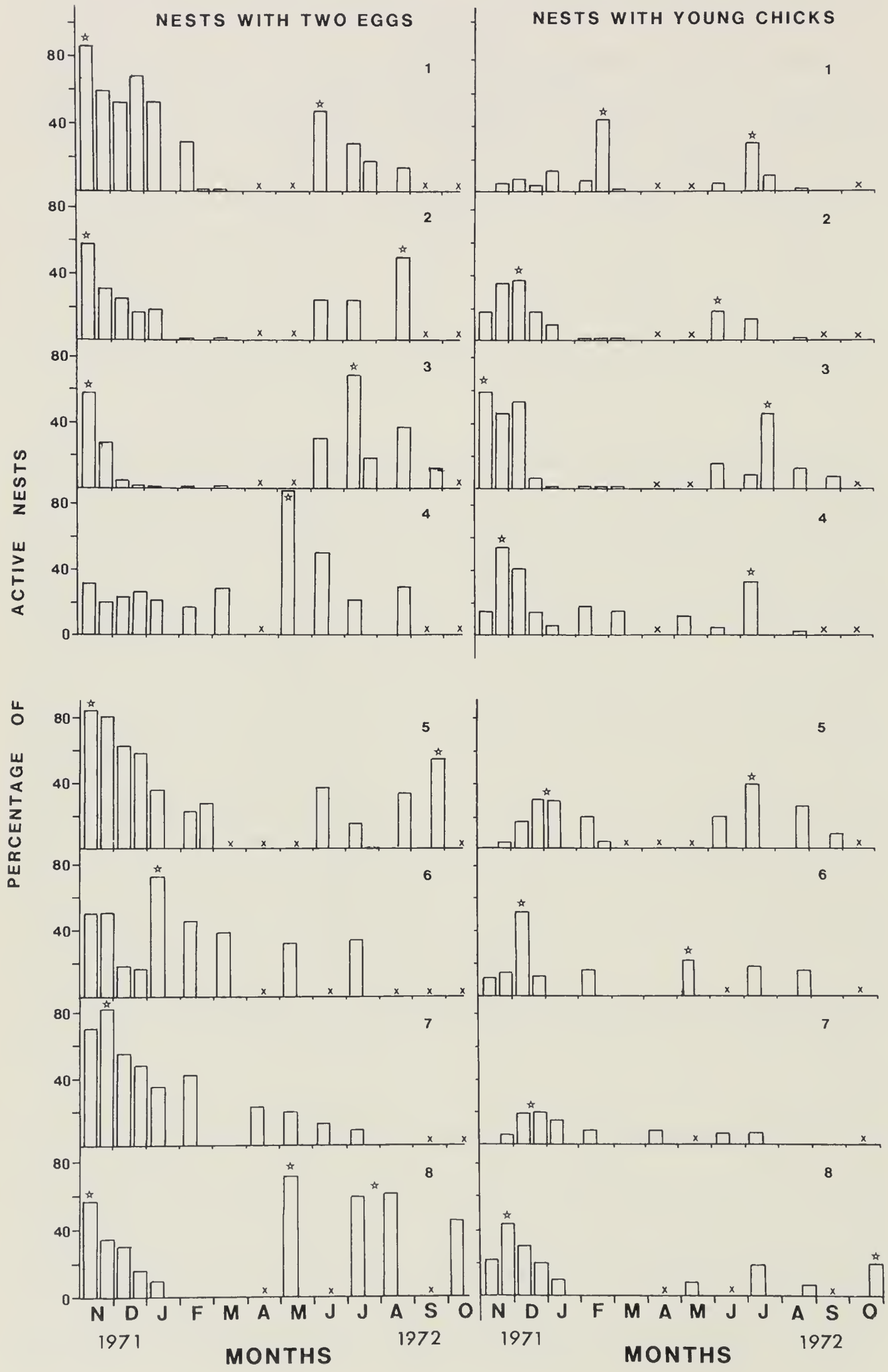
[a] [ ] = predominant stage; NS = not significant; * $P < 0.05$; ** $P < 0.01$ (Chi-square one-sample test).

Two possibilities are apparent when considering the relative proportions of the different stages of breeding represented in the high-density colonies surveyed in 1989: (1) If we assume that there is no breeding peak, we would expect to find birds at all stages of breeding, and in any given colony all stages would be represented equally. This was not so, with seven of the eight colonies sampled showing a significant bias in stages; and (2) If the bias were simply a result of an overall breeding peak, we would expect that the bias in stages would be in a consistent direction and that every colony would reflect the overall frequency of stages. However, we found that the bias was not toward a single stage and that each of the three identified stages predominated in one or more of the study colonies.

Further support for the existence of local synchronizing events comes from the 12-month census data. If we assume that only a seasonal effect exists to produce synchrony, with birds breeding in an optimal "window" of time, we would expect that each colony would show a flattened (platykurtic) distribution of numbers of breeding birds and that the placement of the plateau of the frequency curve would not differ between areas. If local synchrony occurs within the breeding peak, the frequency distribution of breeding birds would be more peaked (leptokurtic). Most birds should breed within the peak time, but the precise location of the breeding peak will vary between areas. The wider the range of peaks between areas, the greater the evidence for local synchrony rather than just a general seasonal effect. Our results show that even when counting proportions of nests with full clutches or downy chicks, rather than the more precise dates of clutch initiation or hatching, a considerable inter-colony variation in the placement of breeding peaks was evident. The total absence of active nests during some census periods throughout the year and the subsequent rapid build-up in breeding numbers confirms the existence of synchronizing factors working at the colony level.

Breeding in a particular colony may become more synchronous if social facilitation of visual displays such as mutual ecstatic, bowing, or copulatory behaviour (Eggleton and Siegfried 1979) occurs. Copulation is socially facilitated in the Adelie penguin (*Pygoscelis adeliae*) (L. S. Davis, pers. comm.). Even in the absence of direct visual contact, vocal displays, too, may cause an increase in the frequency of sexual behavior by conspecifics. Acoustic displays in Little Blue Penguins (*Eudyptula minor*) have been shown to increase the rate at which perceiving conspecifics copulate and perform courtship displays (Waas 1988).

Spatial and temporal clustering of breeding may produce benefits for participating birds apart from those relating to optimal foraging conditions. Enhanced success for peak-breeding


NESTS WITH TWO EGGS
NESTS WITH YOUNG CHICKS
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1
2
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birds may be due to such factors as improved incubation, decreased desertion (Spurr 1977), reduced predation through predator satiation (Darling 1938) or group aggressive defense (for review see Gochfeld 1980).

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Fig. 2. Percentage of nests containing: (a) a full clutch of two eggs, and (b) one or two small downy chicks, in eight Jackass Penguin colonies over a 12-month period (November 1971–October 1972). Stars indicate breeding peaks.

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Characteristics of Yellow-crowned Night-Heron nests in lowland hardwood forests of Missouri.—Published information on the nesting ecology of many Ardeids is largely restricted to coastal areas and consists of qualitative descriptions of specific nest sites (Eyles 1938, Ralph and Ralph 1958, Maxwell and Kale 1977). However, application of quantitative multivariate techniques, in conjunction with behavioral observations, has led to the supposition that subtle but significant differences in nest-site characteristics exist between species within a colony (Beaver et al. 1980). Limited information also is available regarding intraspecific differences in nest-site characteristics caused by shifts in vegetation communities between physiographic regions (McVaugh 1975, Bagley and Grau 1979).

Yellow-crowned Night-Herons (*Nyctanassa violaceus*) often nest alone or scattered in loose aggregations (Parnell and Soots 1979). Studies in coastal areas indicate that nest-site characteristics of Yellow-crowned Night-Herons vary and may depend on several factors, including vegetation structure and social conditions (e.g., presence of other heron species). In swamps, nests often are positioned over water in understory vegetation (Wischusen 1979). Nests also have been reported in hardwood timber (Price 1946, Sutton 1967) and in pines (*Pinus* spp.) (Wayne 1906, Watts 1989). In mixed-heron colonies, night-herons tended to nest on the ground (Burger 1979).

Regardless of social conditions or the type of macrohabitat selected, minimizing exposure to avian predators (Burger 1978) or inclement environmental conditions (Beaver et al. 1980) appears to be a common feature of nest position. This hypothesis has been used to explain the placement of nests low in tree canopies (Watts 1989). The goals of this study were to examine the variability in vegetation characteristics among Yellow-crowned Night-Heron nest sites detected in a lowland hardwood wetland and to evaluate the similarity between the vegetation characteristics useful in describing Yellow-crowned Night-Heron nest sites in coastal and inland wetlands.

Study area and methods.—The study was conducted in the Mingo Swamp of southeastern Missouri, the largest remaining tract of lowland hardwood wetlands in the state (Korte and Fredrickson 1977). Situated at the northern terminus of the Mississippi alluvial delta, Mingo Swamp encompasses about 9312 floodable ha. Mingo National Wildlife Refuge (MNWR) and adjacent Duck Creek Wildlife Management Area (DCWMA) are charged with management responsibility of these lands. A series of wells and ditches are used to manipulate water levels within marshes and leveed impoundments, primarily for waterbirds. Approximately 637 ha are managed for the production of moist-soil vegetation or row-crops, 6038 ha as forested impoundments (live forest = 4502 ha, dead tree = 456 ha, scrub/shrub = 550 ha, and greentree reservoir = 530 ha), and 1476 ha as marsh (Heitmeyer et al. 1989).

Searches for Yellow-crowned Night-Heron nests were conducted from April through August of 1989 and 1990. Nests were located by walking systematic transects through about 500 ha of contiguous forested impoundments and searching specific areas where Yellow-crowned Night-Heron activity had been reported in past years. Within forested areas, open areas resulting from clearcuts and thinning operations also were searched. Based on 1983 information (Heitmeyer et al. 1989), about nine percent of the macrohabitats (i.e., live forest, greentree reservoir, and scrub/shrub) potentially suitable for nesting by Yellow-crowned Night-Herons were surveyed. Openings within forested habitats represented about 2% (10 ha) of the surveyed area. Nest trees were mapped, labeled as to year of activity, and visited periodically to confirm the use of nests by Yellow-crowned Night-Herons.

Nine vegetation characteristics were recorded at each nest site (Table 1). Height of the nest tree and the nest were measured to the nearest 0.5 m at a horizontal distance of 20 m from the nest tree, using the Bitterlich angle method. Diameter at breast height (dbh) of the

TABLE 1
CHARACTERISTICS OF 33 YELLOW-CROWNED NIGHT-HERON NEST SITES IN MINGO SWAMP, SOUTHEASTERN MISSOURI

Variable	$\bar{x}$	SE	Range
Nest tree			
Height (m)	29.1	0.7	20.0–35.5
Diameter breast height (cm)	52.8	2.9	27.0–87.0
Horizontal nest position (%)[a]	73.6	1.8	50.0–87.0
Nest height (m)	18.3	0.6	10.5–25.0
Nest branch angle (°)	77.0	1.3	60.0–90.0
Habitat			
Tree density			
Poletimber (trees/ha)	920	98	200–2400
Sawtimber (trees/ha)	139	14	50–400
Total trees (trees/ha)	1059	95	350–2500
Basal area (ms^2/ha)	22.8	0.9	10.3–32.1

[a] Calculated as 100 × distance of nest from tree center/nest branch length.

nest tree was determined with a Biltmore stick. Basal area was measured using a 10 BAF prism with the nest tree as the center of a variable radius plot. An index of nest position relative to canopy breadth (distance of nest from tree center/nest branch length) × 100 was calculated as was the angle of the nest branch. Tree density was measured within a 0.02-ha circular plot with the nest tree at plot center. Distance to the nearest adjacent nest within each nest aggregation also was recorded.

Data among years were combined prior to analyses because of the small number of nests located. Tree preference was examined by Chi-square analysis using data on tree diversity and density collected within discrete 0.0-2ha plots. Factor analysis (FA) with the VARIMAX rotation method was used to reduce the number of structural features needed to describe nest-site characteristics.

Results.—Twenty-three nests were located in 1989 and 10 additional nests in 1990. Maps of nest locations indicated five and three loose colonies in 1989 and 1990, respectively. The three colonies located in 1990 occupied sites used in 1989. The maximum mean distance between nests comprising a colony was 74 m, whereas the minimum distance between colonies was about 350 m, providing evidence that nests were not randomly distributed. Colonies were comprised entirely of Yellow-crowned Night-Heron nests and averaged 4.6 ± 1.2 (SE) nests in 1989, 3.67 ± 0.9 nests in 1990, and 4.25 ± 0.8 nests across both years of the study. Mixed-species colonies were not detected. Four of the colonies were on the DCWMA in forested sites that are leveed and managed as greentree reservoirs. One colony was in a shallow forested drainage on MNWR. In general, areas containing Yellow-crowned Night-Heron nests were characterized as sawtimber stands with moderate to sparse understories and sparse ground cover. No nests were located in small clearcuts or thinned areas within the forested impoundments, but the area surveyed was small.

Although three of the colonies were located in both 1989 and 1990, only three trees were used as nest sites in both years. No trees were occupied by more than one pair in the same year. Nests were located in five different tree species. Thirty-two nests (97%) were in oaks; 19 (58%) in pin oak (*Quercus palustris*), five (15%) in overcup oak (*Q. lyrata*), and four

TABLE 2
CHARACTER LOADINGS ON THE FIRST THREE PRINCIPAL FACTORS AFTER VARIMAX ROTATION OF THE FACTOR MATRIX

Character	Component		
	Stand density	Nest position	Stand structure
Diameter breast height (cm)	0.23	0.40	−0.46
Tree height (m)	−0.27	0.76	−0.17
Nest height (m)	0.16	0.88	0.08
Nest branch angle (°)	−0.18	0.36	0.58
Basal area (m^2/ha)	0.26	−0.15	0.81
Horizontal nest position (%)	0.31	0.70	−0.01
Sawtimber/ha	−0.16	−0.04	0.81
Poletimber/ha	0.96	0.09	−0.14
Trees/ha	0.97	0.09	−0.02
Variance explained (%)	29.5	20.9	19.8

(12%) each in shingle oak (*Q. imbricaria*) and black oak (*Q. velutina*). One nest (3%) occurred in sweetgum (*Liquidambar stryraciflua*). Other species of trees within an 8-m radius (0.02-ha) of nest sites included shagbark hickory (*Carya ovata*) and blackgum (*Nyssa sylvatica*); snags also were present. Based on the density of each tree species within 0.02-ha of nest sites, nests were constructed in oak species significantly more than expected ($\chi^2 = 16.6$, 1 df, $P < 0.005$) by chance based on their occurrence.

Three uncorrelated linear combinations of habitat variables, identified by factor analysis, accounted for 70.2% of the variation in nest-site attributes (Table 2). The first factor, or combination of variables, was denoted as stand density. The variables with the highest loadings were poletimber and total tree density. Both variables were highly variable among nest sites. Poletimber density at individual nest sites ranged from 200–2400 trees/ha ($\bar{x} = 920 \pm 98$), whereas total tree density ranged from 350–2500 trees/ha ($\bar{x} = 1059 \pm 95$) (Table 1).

The second factor was denoted as nest position because the variables with the highest loadings were nest height, horizontal position of the nest, and tree height (Table 2). The first two variables are dependent on tree form, of which tree height is a partial indicator. The height of the nest varied directly with the height of the nest tree ($r = 0.54$, $P = 0.001$), with the vertical position of the nest about 9–11 m below the maximum tree height (Table 1). Horizontally, nests were located away from the tree bole and towards the edge of the canopy. All nests were located on the outer half of the limb forming the main nest brace.

The variables with the highest loading coefficients on the third axis were basal area and sawtimber density (Table 2). This factor was termed stand structure because it partially describes the size and density of potential nest trees. Sawtimber density ranged from 50–400 trees/ha ($\bar{x} = 139 \pm 14$) at individual nest sites. Basal area, measured in variable radius plots, also indicated that several trees in the sawtimber size class were in the vicinity of the nest site.

Discussion.—The average size of colonies in our study was 4.25 ± 0.8 nests, and all nests occurred in separate trees. This provides additional support of earlier evidence that night-herons typically nest in unshared trees (Wischusen 1979, Drennen et al. 1982) and that

colonies are small relative to other Ardeid colonies (Custer et al. 1980, Palmer 1962, Hancock and Kushlan 1984).

Yellow-crowned Night-Herons are known to use a variety of habitats for nesting (Watts 1989), and the influence of social and vegetation factors in nest-site selection has been documented for other heron species (McCrimmon 1978, Burger 1979, Beaver et al. 1980). An additional factor in inland freshwater systems may be the distance to reliable foraging areas during brood rearing. In coastal environments, foraging tends to be dependent on tidal fluctuations (Custer and Osborn 1978, Watts 1988), but the location of these areas is dependable. In contrast, the location of available foraging sites in Mingo Swamp is more dynamic (Laubhan et al. 1991). Water levels within leveed impoundments fluctuate seasonally as a result of planned management activities. Water may be present in an impoundment when nest sites are selected but may be dry two weeks later. As a result, foraging opportunities only are available for a short time. On DCWMA and MNWR, individual impoundments are drawn down sequentially so that foraging opportunities last longer, but the location of foraging sites changes periodically. This may influence colony location among years, but insufficient data were collected to permit testing this hypothesis.

Because wetland vegetation is primarily determined by the hydrological regime (Fredrickson and Reid 1990), the species of nest tree partially reflects the long-term hydrological cycle in the vicinity of the nest. Pin oak predominates in habitats that remain partly flooded from December to May, and surface water is rarely >20 cm deep (Heitmeyer et al. 1989). In addition to providing good nesting substrate, more nests may have occurred in pin oak because this species is adapted to sites that are indicative of favorable foraging areas that are available through the brood rearing period.

Several hypotheses have been provided to explain the position of heron nests in the tree canopy. Positioning nests low in the canopy of hardwood trees reduces the danger of excessive thermal stress during the brood period (Burger 1978, Beaver et al. 1980) and also may provide concealment from aerial predators (Burger 1978). In Virginia, Yellow-crowned Night-Herons nested low in the canopy of loblolly pines (*P. taeda*). The primary selective advantage of pines over hardwoods may have been to reduce clutch losses to crows (*Corvus brachyrhynchos* and *C. ossifragus*), even though deciduous trees provide a better thermal environment for brood rearing (Watts 1989). These results indicate that positioning nests within a specified zone of the canopy may be a mechanism to increase the recruitment of young.

In our study, both the structural features of nest trees and nest position were highly uniform. In contrast with previous studies, however, we found that nests typically were placed away from the center of the tree and in the upper reaches of the canopy. According to Watts (1989), this may increase the incidence of aerial predation. Although nest fate was not closely documented, crow nests were present in the same tree as Yellow-crowned Night-Heron nests, suggesting that clutch loss to crows may occur. However, it may also suggest that clutch loss to crows is not a principal factor influencing nest-site selection in this area.

The placement of nests in the upper portion of trees and towards the outer edge of the canopy may represent a mechanism to reduce the probability of nonavian predation. Black rat snakes (*Elaphe obsoleta*) destroyed 25% of all nests by box-nesting Wood Ducks (*Aix sponsa*) on MNWR from 1966–1970 and apparently killed two incubating female wood ducks (Hansen and Fredrickson 1990). During the same time period, raccoons (*Procyon lotor*) destroyed an additional 8% of Wood Duck nests (Hansen 1971). The position of night-heron nests observed in our study would tend to minimize the predation risk by terrestrial predators, because nests are more difficult to detect from the ground and from the main stem of the tree following leaf expansion. At the same time, some overhead cover would be provided for shading young and for protection from aerial predators. Nesting in

separate trees also may help reduce the incidence of terrestrial predation by forcing predators to exploit each nest tree individually (Watts 1989).

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Migration of Sharp-shinned Hawks in the Dry Tortugas, Florida.—It is a long-held notion that many species of raptors (Falconiformes) avoid crossing large bodies of water during their biannual migrations (Allen and Peterson 1936, Haugh and Cade 1966, Heintzelman 1986). Recently, however, some species have been found to make long water crossings during migration (MacRae 1985). Kerlinger (1985) suggested that species involved in over-water flights are those with high aspect ratio wings that decrease the cost of powered flight. Species that lack the desired aspect ratio for sustaining flapping flight seem reluctant to undertake long-distance water crossings (Kerlinger 1989). Indeed, one of these species, the Sharp-shinned Hawk (*Accipiter striatus*), seldom undertakes water crossings of >125 km and apparently avoided crossing water when lateral winds were strong and chances of seaward displacement were high (Kerlinger 1989). Large numbers of Sharp-shinned Hawks are observed every fall in the Florida Keys where minor water crossings are routine (e.g., Atherton and Atherton 1988). Although a northeasterly reverse migration has been described from the Keys (Darrow 1983), many birds traverse >100 km of ocean to reach the Dry Tortugas where they can be quite common (W. G. Mattox, pers. comm.). No information, however, has been gathered concerning the flight orientation of these migrants after reaching the Tortugas. Three possibilities exist: (1) they continue on a southerly or southwesterly direction across the Gulf of Mexico, (2) they reverse direction and head easterly back toward the Keys, or (3) they reorient in a northwesterly direction toward Louisiana and Texas. I undertook this study to determine the directional orientation and behavior of Sharp-shinned Hawks confronted by the open waters of the Gulf of Mexico at the Dry Tortugas.

The Dry Tortugas, 117 km west of Key West (24°38′N, 82°52′W), form the western

terminus of the Florida Keys. The Marquesas Keys, 83 km to the east, are the nearest point of land. Cuba lies 150 km to the south and the Yucatan Peninsula lies 560 km to the southwest. The islands, ranging from a small, shifting sandbar to the remains of Fort Jefferson on 2.6 ha Garden Key, are administered by the National Park Service. Observations were made on Garden Key from 5 October to 7 October 1988. The ramparts of Fort Jefferson allowed for 5 km visibility in all directions. Five 1-h sampling periods were selected randomly from periods starting at 09:00 h and ending at 17:00 h. Observations were made by scanning 360° from the fort's ramparts with a 10× binocular. Species, age, and time of each passing hawk were recorded. I also recorded the approaching direction of the bird and the direction the bird was heading after passing the fort. Birds were followed for 0.5 km as they passed the fort. Flight behavior was recorded as flapping, flap-gliding, or static soaring, and the altitude of flight was assessed according to the Hawk Migration Association of North America's guidelines (HMANA no date). Wind speed, determined by wind gauge, and wind direction were recorded at the start of the hour. Opportunistic observations of over-water flight behavior were also collected.

Six species of hawks (N = 136) were recorded on Garden Key. Sharp-shinned Hawks dominated the observations (75%). Of these, 98% (N = 101) were immatures. Additional species encountered on the Tortugas included American Kestrels (*Falco sparverius,* 12%), Peregrine Falcons (*F. peregrinus,* 7%), Merlins (*F. columbarius,* 4%), Northern Harriers (*Circus cyaneus,* 1%), and Broad-winged Hawks (*Buteo platypterus,* 1%). The rate of passage of all species averaged 25 birds/h; Sharp-shinned Hawks averaged 19 birds/h. Wind speeds, ranging from eight to 24 km/h, were rather invariant, and wind direction was consistently from the northeast. All Sharp-shinned Hawks employed a flap-flap-glide method of flight. Temporarily abandoning powered flight when encountering the fort, hawks briefly soared in updrafts caused by the 16 m high walls. Most individuals migrated at altitudes between five and 30 m. Few Sharp-shinned Hawks reoriented northward or reversed their migration to the east. The majority (86%, N = 101) of sharp-shins pursued a westerly route, mainly at a heading of 270°. Birds not heading west were generally flying eastward (14%, N = 101), retracing their trip down the keys. Not once did a bird reorient northwesterly toward the Louisiana or Texas coast. Passage rate of Sharp-shinned Hawks significantly declined throughout the day (Kendall's concordance test; $r_k = 0.80$, $P = 0.042$, N = 5). Additionally, a significantly higher proportion of Sharp-shinned Hawks headed west in the morning than in the afternoon (large sample z-test for proportions; $z = 4.03$, $P \leq 0.0001$, N = 97). In contrast, falcons did not head west significantly more often in the morning than in the afternoon (large sample z-test for proportions; $z = 1.23$, $P \geq 0.183$, N = 26).

My results suggest that Sharp-shinned Hawks are deliberately initiating an over-water flight across the Gulf of Mexico. No birds reoriented and few reversed migration. Because birds arrived at the Tortugas on northeasterly winds, they were not the product of northwesterly wind displacement as were water crossing sharp-shins on the Atlantic coast (Kerlinger 1989). If sharp-shins decide to cross the Gulf of Mexico directly to Central America, the shortest distance lies between the Tortugas and the Yucatan peninsula. Although flying due west (270°), northeasterly winds would make the realized track of birds more southwesterly and deliver them on the Yucatan peninsula. Traveling at ≥11 mps (Kerlinger 1989), sharp-shins would need 14 h to accomplish this crossing. Initiating an over-water flight early in the day might maximize the success of an over-water flight. Attempting a flight on a day with tail winds, which maximizes flight distance (Kerlinger 1989), and incorporating an energy-saving flap-glide style of flight instead of flapping style of flight might also help ensure success. This contrasts to falcons whose increased powered flight efficiency may enable them to be less selective in choosing departure times and, as do peregrine falcons, even engage in nocturnal migration. After leaving the Tortugas, Sharp-shinned Hawks might shorten the

over-water flight by adjusting their heading toward Cuba. Island-hopping to Cuba would reduce length of the water crossing by 50% of the direct over-water flight distance to the Yucatan peninsula. However, migrant sharp-shins are only rarely recorded in Cuba (Palmer 1988).

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Bird species on St. Andrew and Old Providence Islands, West Caribbean.—The Islands of St. Andrew and Old Providence (as called by their inhabitants), or San Andrés and Providencia as called by Colombia which governs them), lie in the SW Caribbean about 200 km east of Nicaragua, comparatively isolated from the rest of the West Indies. These oceanic islands have a resident bird fauna of 16 species, mainly of West Indian affinities (Bond 1950, 1988). The two islands are separated by about 100 km, and many of the birds resident on both are represented by different subspecies on each (Bond 1950).

Old Providence is about 8 × 5 km, with a 1-km diameter islet, St. Catherine (Santa Catalina), off its northern end. It is volcanic, with steep hills, several rising to between 350 and 400 m. The coast is mainly rocky with small sandy beaches, many backed by dry mangrove woodland, which merges with dry thorn woodland as the land rises. Much of the

lowlands have been converted to cattle pasture or farmland, but extensive dry woodland remains on the main island and on St. Catherine. The upper slopes of the hills, especially in the south, are largely clothed with native forest, and the island is not "most(ly) . . . deforested and devoted to cattle ranching" as stated by Hilty and Brown (1986).

By contrast, St. Andrews is a low coral island about 13 × 4 km, rising to only 100 m along its central ridge. Most of the island is urbanized (northernmost 20%) or converted to coconut plantations (southern half), with farmland in between. Native vegetation is restricted to small patches of trees and scrub amongst the farmland and settlements.

Early visits by ornithologists are listed by Bond and Meyer de Schauensee (1944). Subsequently, both islands were visited in 1948 by Bond (1950) and in 1972 by Russell et al. (1979), while St. Andrew was visited in 1966–1967 by Barriga et al. (1969) and Paulson et al. (1969) and in 1983 by Nash (Barlow and Nash 1985).

We visited the islands from 26 February to 5 March 1989, with five days (27 February–3 March) on Old Providence and the remainder on St. Andrew. Since Bond's visit in 1948, the only documented ornithological results from Providence were by Russell et al. (1979) who spent two days there in April 1972. We had adequate time on Old Providence to examine all major habitats except the extensive mangroves below the airport on the east coast. We spent only one afternoon (26 February) and one day (4 March) observing birds on St. Andrew, visiting the town and harbor, shoreline along the north and east coast (mainly sandy, with rocky areas), El Cove on the west coast, and coconut plantations, farmland, and patches of native vegetation in the interior. However, our visit to St. Andrew was too short to sample the avifauna adequately.

We use the following conventions: very abundant—>100 seen or heard in suitable habitat per day; abundant—11–100; common–10; frequent–several may be seen but not every day; records of rarer species are given in full detail. Where a subspecific name is used, the subspecies is endemic to the islands.

Resident Species

White-crowned Pigeon (*Columba leucocephala*). Abundant in dry woodland and hill forest on Old Providence (P). Not seen on St. Andrew (SA).

White-winged Dove (*Zenaida asiatica*). On P, Very abundant in all types of woodland, also seen in gardens and flying over fields. One seen SA, north central area.

Mangrove Cuckoo (*Coccyzus minor abbotti*). Common in dry woodland on P, where seen courtship feeding and copulating. Not seen SA. Bond (1950) also found it common on P and "rather rare" on SA, while it was not seen at all by Paulson et al. (1969) or Russell et al. (1979).

Smooth-billed Ani (*Crotophaga ani*). Common in farmland on P (rare according to Russell et al. 1979). Not seen SA. Thought by Bond (1950) to have arrived on the islands about the early 1940s; the first probable sight record was in 1941 (Bond and Meyer de Schauensee 1944).

Green-breasted Mango (*Anthracothorax prevostii hendersoni*). Common on P in dry woodland and gardens. Two seen SA, north central area.

Caribbean Elaenia (*Elaenia martinica cinerescens*). Abundant in dry woodlands and hill forest on P. Not seen SA.

St. Andrew Mockingbird (*Mimus magnirostris*). (Species endemic to SA; by some regarded as a race of Tropical Mockingbird [*M. gilvus*].) Common in north central area in scrub, farmland and gardens.

St. Andrew Vireo (*Vireo caribaeus*) (species endemic to SA; there are no records for P, contrary to Hilty and Brown 1986). Common in undergrowth of shrubby areas in north-central area.

Thick-billed Vireo (*V. crassirostris approximans*). Abundant in shrubby areas, dry woodland, and hill forest. There are no records for SA, contrary to Hilty and Brown (1986).

Black-whiskered Vireo (*V. altiloquus grandior* [P]; *V. a. canescens* [SA]). Only one seen on P, in dry woodland. None seen SA.

Bananaquit (*Coereba flaveola tricolor* [P]; *C. f. oblita* [SA]). On both P and SA very abundant in all habitats with trees or bushes. On P seen carrying nest material and visiting complete nests.

Jamaican Oriole (*Icterus leucopteryx lawrencii*) (SA only). One seen in trees edging a field and banana plantation, north central area.

Black-faced Grassquit (*Tiaris bicolor grandior*). Abundant throughout P in open vegetation and along roadsides; seen feeding fledglings. Very abundant SA in all open habitats including farms, plantations and roadsides.

The following three resident species, two of which have also been recorded as migrants, were not found by us: Green-backed Heron (*Butorides striatus*) (both islands); Caribbean Dove (*Leptoptila jamaicensis neoxena*) (SA); Yellow Warbler (*Dendroica petechia armouri*) (P), (*D. p. flórida*) (SA). It is surprising that the Green-backed Heron and Yellow Warbler eluded us on Old Providence, the only resident species to do so. We visited several coastal and mangrove areas and would have expected to have found such a noisy, conspicuous bird as the Green-backed Heron. The endemic subspecies of the Yellow Warbler was reported by Bond (1950) to be one of the rarest resident birds on Old Providence, and Russell et al. (1979) also failed to find it. Some concern might be expressed about the survival of this well-marked race. The endemic race of the Black-whiskered Vireo also seems rare (only one individual seen) and must therefore be vulnerable to extinction.

Given the brevity of our visit to St. Andrew, it is not surprising that we failed to locate these three species and others on that island.

Other apparent changes in status since the visit of Russell et al. (1979) concern the two cuckoos. The Mangrove Cuckoo was not found by Paulson et al. (1969) or Russell et al. (1979), but we found it to be common on Old Providence. Considering the amount of time spent by Paulson et al. and Russell's party on St. Andrew and the shortage of its apparently preferred habitant (dry woodland and mangroves) there, it seems possible that the St. Andrew population may no longer exist. However, the population on Providence seems healthy at present. The Smooth-billed Ani, thought rare by previous visitors, now seems well-established on Old Providence.

Nonresident Species

Presumed non-resident species recorded during our visit include three species not previously documented from either island, all here recorded on Old Providence. One Parasitic Jaeger (*Stercorarius parasiticus*) was present in the shallows between Providence and St. Catherine, 27–28 February. Its occurrence on Providence is not unexpected; it is a species which might be expected to wander occasionally to that part of the Caribbean. A Scarlet Macaw (*Ara macao*) was seen free-flying and apparently wild, away from human habitation, near Southwest Bay. It seems most likely to have been an escape from captivity, but the nearest mainland source area is Nicaragua, only 200 km away, from where Bond (1950) presumed that the resident Green-breasted Mango originated.

We found Yellow-green Vireos (*V. flavoviridis*) to be common in dry woodland in the lowlands of Providence. The birds were watched at close range and could be clearly distinguished from the similar but much larger resident races of Black-whiskered Vireo by their size, short bills and lack of malar streak. A Red-eyed Vireo (*V. olivaceus*) was collected on 31 March 1941, on Albuquerque Keys (12°12′N, 81°50′W, 40 km SSW of St. Andrews) (Bond and Meyer de Schauensee 1944), but the birds we saw were referred to Yellow-green

Viro by their green upperparts, yellow on underparts, and lack of dark outline to the creamy-white supercilium. Further, the migration of Red-eyed Vireo probably occurs later in the spring (Skutch 1960). The lack of previous records of Yellow-green Vireo on Providence could be due to previous visits by ornithologists not having coincided with the peak migration time (e.g., Bond 1950) or being of short duration (Russell et al. 1979). However, Yellow-green Vireos breed in Central America and do not appear to have been recorded previously in the West Indies. They may be regular migrants on St. Andrew and Old Providence.

We recorded six additional species which were not previously known on Old Providence and two additional species not formerly reported from St. Andrew. On Providence we recorded Brown Pelican (*Pelecanus occidentalis*) (one present 27 February–1 March in shallows between Providence and St. Catherine), Cattle Egret (*Bubulcus ibis*) (common in open areas, especially grassland), Yellow-crowned Night-Heron (*Nyctanassa violacea*) (frequent in mangroves, especially on St. Catherine), Willet (*Catoptrophorus semipalmatus*) (frequent around the coast), Tennessee Warbler (*Vermivora peregrina*) (one in dry woodland), and Common Yellowthroat (*Geothlypis trichas*) (one in dry woodland). On St. Andrew, we found Greater Yellowlegs (*Tringa melanoleuca*) (one at El Cove) and Black-throated Green Warbler (*Dendroica virens*) (one in scrub).

Most non-resident land birds were found in the dry woodland at low altitude, where we spent much observation time. Very few species were found in the hill forests. Although we spent only one day at higher altitude, we formed the impression that bird densities were lower there. We saw very few migrant warblers in the hill forest but many in the dry woodland just below it, on the same day. Further, resident birds seemed less common in the hill forest.

Previous authors have listed all herons but the Green-backed Heron as non-resident, although it seems more likely that some are resident breeders. This particularly applies to the Cattle Egret and Yellow-crowned Night-Heron, both of which are now known to occur on both islands and which are present in good numbers. The remaining species which we report from one or other of the islands for the first time, apart from the Brown Pelican, are Nearctic migrants, either shorebirds or warblers.

Assuming that the seabirds and herons (apart from the Green-backed Heron) are not resident, our records bring the total of non-resident birds recorded from the islands to 81 (57 on Old Providence, 72 on St. Andrew) with 12 residents on Providence and 15 on St. Andrews. The number of new non-resident species found per ornithological visit seems to be declining on St. Andrew (unpubl. data), indicating that the total number of non-resident species which visit it regularly is about 70. By comparison, Old Providence appears understudied, and it is likely that it will eventually be found to hold as many regular non-residents as St. Andrew, perhaps more, considering that it has a greater variety of habitats and more natural woodland.

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Body measurements of Boreal Owls in Idaho and a discriminant model to determine sex of live specimens.—The recognized distribution of Boreal Owls (*Aegolius funereus*) in North America has expanded significantly in the past seven years (Palmer and Ryder 1984, Hayward et al. 1987, O'Connell 1987, Stahlecker and Rawinski 1990). As interest in the Boreal Owls of the western United States increases and population studies become important in assessing species status, reliable identification of sex and age will be useful. Here we report the body measurements of 58 adult Boreal Owls captured in Idaho and describe a discriminate model for sexing the birds.

During studies of Boreal Owl habitat use in 1980–1987, we captured and measured 14 male and 11 female Boreal Owls in Chamberlain Basin of the Frank Church—River of No Return Wilderness of central Idaho. We captured the owls at night, on bal-chatri traps or in mist nets at calling sites during winter and spring. We recaptured and remeasured some individuals when their radio-transmitters needed replacing. During an associated investigation evaluating nest boxes as a tool to monitor Boreal Owl populations, we captured and measured eight males and 24 females at nest boxes near McCall, Idaho from 1988–1990. We captured an additional female at a nest box in northern Idaho in 1989.

Because the owls at Chamberlain Basin were radio marked, we could observe their behavior during courtship and nesting and thereby determine each bird's sex. Owls observed singing the staccato song (Bondrup-Nielsen 1984) and/or seen delivering prey to a nest cavity occupied by another Boreal Owl were classified as males. Owls that incubated eggs, brooded young, or otherwise occupied a cavity day and night for at least a week were classified as females (Mikkola 1983). Similarly, owls captured during the nest box study were classified by behavior.

We weighed owls with a 300-g Pesola scale to the nearest g. A wing tracing was made without overextending the wing and its area was measured using a planimeter. We recorded wing length (wing chord) as the distance from the carpal region of the bent wing to the tip

Table 1

Body Measurements of Boreal Owls in Idaho. Sample Includes 58 Individuals with Repeated Measures of Some Birds Captured More Than Once over Five Years

Variable	Male				Female			
	Mean	SE	Range	N	Mean	SE	Range	N
Weight (g)	117.3	1.39	93–139	(50)	166.8	2.46	132–215	(53)
Bill (mm)	12.7	0.112	11.2–14.0	(40)	13.5	0.094	11.8–14.6	(42)
Wing area (cm^2)	237.2	2.92	199–272	(35)	269.3	3.58	229–299	(28)
Wing loading (g/cm^2)	0.50	0.011	0.36–0.66	(33)	0.62	0.011	0.49–0.75	(28)
Wing length (mm)	172.5	0.58	163–179	(41)	183.6	0.72	174–198	(49)
Eighth primary (mm)	134.4	0.57	127–141	(35)	142.9	0.56	134–150	(43)
Alula (mm)	48.6	0.41	41–53	(41)	52.5	0.56	41–60	(48)
Tail (mm)	99.9	0.54	91–107	(44)	106.0	0.69	95–117	(45)
Foot (mm)	34.0	0.15	32–35	(22)	36.7	0.34	33–39	(23)

of the longest primary without flattening the wing (Pettingill 1970:448). We measured the tail, alula, and eighth primary (the longest) by slipping a ruler under the feather to its base. We did not flatten the eighth primary but did for the alula and tail. Bill was measured with calipers from the tip to the top of the nostril. We did not measure to the cere (Pettingill 1970:447) because that measurement varied due to injuries. We measured feet by stretching diagonal toes open and measuring from the tips of the pads (i.e., talon excluded).

Boreal Owls are one of the most dimorphic owls (Earhart and Johnson 1970, Mueller 1986, Norberg 1987). Our results confirm substantial differences in body measurements between sexes (Table 1). Mean mass, bill length, alula, eighth primary, wing length, wing area, tail length, and foot length for females exceeded those for males (*t*-test, $P < 0.0005$ for all measures). We did not find a difference in mean weight of male or female owls between summer and winter seasons (*t*-tests, $P = 0.15$, male; $P = 0.324$ female). Here we define summer as 1 May–1 November.

Our measurements fall within the ranges reported by other authors, although we found significant differences in mean values for some morphological measurements (measures of variance were not published in many cases, so tests of differences are not possible in all cases). Korpimaki (1981) reported tail lengths. His averages were 105.3 mm for males (N = 27) and 109.6 mm for females (N = 106) which were larger than ours (*t*-test, $P < 0.0001$, $P = 0.006$, respectively). Dement'ev and Gladkov (1954) reported wing lengths but not standard deviations for four Russian subspecies. Males averaged 163 mm (*A. f. funereus*) (N = 21), 166.2 mm (*A. f. sibiricus*) (N = 19), 180 mm (*A. f. magnus*) (N = 6), and 165 mm (*A. f. pallens*) (N = 3). Females averaged 174.7 mm (N = 34), 176.1 mm (N = 23), 187 mm (N = 3), and 167 mm (N = 3) for the respective subspecies. Earhart and Johnson (1970) reported wing lengths of museum specimens for North American Boreal Owls which averaged 161.5 mm for males (N = 10) and 174.4 mm for females (N = 5). Our wing lengths were larger than those of Earhart and Johnson ($P < 0.0001$ for both sexes), however, the difference could be due to shrinkage of museum specimens (Mueller 1986). Finnish Boreal Owls captured at nests also had shorter wing lengths (male $\bar{x} = 168.3$, N = 27; female $\bar{x} = 175.5$, N = 106; Korpimaki 1981) than the Idaho population ($P < 0.0001$ for both sexes).

Male weights reported by other authors are: 116 g (*A. f. funereus*) (N = 1) and 109 g (*A.*

f. magnus (N = 1) from the Soviet Union (Demcnt'cv and Gladkov 1954); 116–133 g from Europe (Geroudet in Mikkola 1983); 92–115 g ($\bar{x}$ = 102.1 g, N = 28) from Finland (Korpimaki 1981); and 85–119 g ($\bar{x}$ = 101.6 g, N = 5) for North America (Earhart and Johnson 1970). Female weights from other populations are 177 g and 197 g (*A. f. funereus*) (Demcnt'ev and Gladkov 1954); 150–197 g (Geroudet in Mikkola 1983); $\bar{x}$ = 170.3 g (N = 157) (Korpimaki 1981); and $\bar{x}$ = 139.5 g (N = 4) (Earhart and Johnson 1970). The weights reported by Earhart and Johnson (1970) arc significantly less than mcan weights for Idaho male and female Boreal Owls (*t*-test, $P = 0.0006$, $P = 0.0012$, respcctively). Weights of female owls in Finland, however, were similar to the Idaho population (*t*-test, $P = 0.2428$), while Finnish males were smaller than the Idaho population (*t*-test, $P < 0.001$).

To develop an objcctive classification of Boreal Owl sex, we performed a discriminant analysis (Johnson and Wichern 1982). To define the initial discriminant function, we included one set of measurements for each owl captured at Chamberlain Basin (N = 25) and a random sample of half the owls caught during the nest box studies (N = 16). Two data sets were used to assess the performance of the discriminant function in classifying the sex of Boreal Owls. Onc test data set (Test I) included the original sample used to form the discriminant model. The second test data set (Test II) included the remaining Boreal Owls captured at nest boxes near McCall, Idaho (N = 16) and repeated measures of owls captured at Chamberlain Basin (N = 22). We feel the repeat measurements from owls at Chamberlin add valuable data to the test. Although these data were not completely independent of the initial classification data, they did incorporate measurement variation, which although frequently ignored as a source of error, is quite large (Mueller 1986). Furthermore, many of these owls were recaptured in different years, and variation between measurements on individual owls was similar to variation among owls. For example, tail length of one female ranged from 100 to 112 mm, a large proportion of the range for all females 95–117 mm.

Wing area, foot length, and eighth primary length were the most difficult measures to take from live birds. Therefore, we excluded these measures from the model. Because weight can vary with time of day, prey population conditions, and weather conditions, we felt the best classification system should also exclude weight. A male measured twice in 14 days lost 23 g, illustrating the degree of fluctuation in this measurement.

No single variable or combination of two or three variables (excluding weight) produced a satisfactory classification. Using wing length (wing), bill length (bill), alula length (alula), and tail length (tail), a linear discriminant model correctly classified all but one owl in both Test I and Test II. Both individuals were males. Because the model corrcctly classified >95% of the test owls, including 96.9% of the observations which were not used to develop the discriminant model (Test II), we considered the model satisfactory.

The linear equations used to identify sex bascd on this model are: female discriminant score (DS) = (16.12wing) + (6.78tail) + (39.11bill) + (4.25alula) − 2198.64; male DS = (15.35wing) + (6.25tail) + (36.83bill) + (3.98alula) − 1965.11. The higher score rcpresents the sexual classification.

The classification model dcscribed above requircs body measurcmcnts which may not have been taken for Boreal Owls in othcr studics. Wc thercforc offcr a second modcl bascd on three common measurements. This modcl must bc uscd with caution becausc it includes owl weight as a variable.

The linear equations used to idcntify sex bascd on this model arc: female DS = (1.82weight) + (15.46wing) + (30.06bill) − 1766.45; malc: DS = (1.52wcight) + (14.41wing) + (27.97bill) − 1510.91. The higher score identifies the owl's sex. This modcl achicvcd 100% correct classification of both test data sets, and separation betwcen groups (generalizcd squared distance = 27.4) was very high.

Because our discriminant classifications are based on only two populations, they must be

used with caution at increasing distances from our study site. Molting birds cannot be sexed using these functions, so biologists should carefully examine birds captured in late summer and autumn.

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Effects of Red-crested Pochard nest parasitism on Mallards.—Although nest parasitism (i.e., a female laying eggs in the nests of others) has been recorded in many waterfowl species (e.g., Weller 1959, Bezzel 1961, Eadie et al. 1988, Rohwer and Freeman 1989), only a few studies have been conducted on this aspect of the breeding biology of ducks (e.g., Weller 1959, Joyner 1976, Sugden 1980, Talent et al. 1981, Amat 1985a). Despite this, it is still not clear to what extent nest parasitism is detrimental to the host. Here I document the effects of nest parasitism by Red-crested Pochards (*Netta rufina*) on Mallards (*Anas platyrhynchos*) and discuss my findings in relation to those of Talent et al. (1981), who studied nest parasitism of Mallards by Redheads (*Aythya americana*).

Study site and methods.—I conducted field work in the marshes of the Guadalquivir (SW Spain) during 1977–1978 and 1984–1989. For a description of the area and methods see Amat (1982, 1985a, b). In these marshes, the nesting season of Mallard is longer than that of the Red-crested Pochard (Amat 1982). The latter species nests mainly on old watercourses which are covered by *Arthrocnemum glaucum* and *Juncus subulatus*. This habitat type is also used by nesting Mallards, mainly during the peak nesting season of the Red-crested Pochard (Amat 1982, 1985b).

Nests were considered intraspecifically parasitized when: (1) more than one egg was laid per day, (2) eggs were added after incubation started, and/or (3) nests contained more than 14 eggs (e.g., Morse and Wight 1969).

In most studies of nest parasitism among ducks, mean clutch sizes of parasitized and unparasitized nests were compared when analyzing the effects of nest parasitism on the host, and some of these studies concluded that clutch sizes of hosts were reduced in parasitized nests (Weller 1959, Joyner 1976, Sugden 1980, Talent et al. 1981, Stoudt 1982, Bouffard 1983). However, laying dates were not controlled for, and this might have led to incorrect conclusions (Amat 1987). The clutch size of Mallards in my study site decreases throughout the nesting season (Amat 1982). Early nesting Mallards (i.e., those with larger clutches) cannot be parasitized by Red-crested Pochards, because the latter species initiates its nesting season later. Thus, it would be inappropriate to include all Mallard nests in the comparisons. Therefore, I restricted the comparison to nests located on the old watercourses (or <10 m from them), because this habitat type was used by Mallards coinciding with the nesting season of Red-crested Pochards, and also because all parasitized Mallard nests were found on this habitat type or very close to it.

Results.—On the old watercourses, Mallard nests (N = 62) were parasitized by conspecifics (1.6%), Red-crested Pochards (30.7%), and Common Moorhen (*Gallinula chloropus*) (1.6%). Furthermore, I found 4.8% of Mallard nests simultaneously were parasitized by Red-crested Pochards and Common Pochards (*Aythya ferina*), and an additional 6.5% simultaneously parasitized by conspecifics and Red-crested Pochards. Only nests exclusively parasitized by Red-crested Pochards are considered in this study.

The fate of nests was similar in parasitized and unparasitized nests (Table 1, $G = 1.77$, $P > 0.05$). The clutch size of Mallards was larger in parasitized than in unparasitized nests (Table 1, $t = 2.38$, $P < 0.05$). The frequency of parasitism in 1988 (50% of 24 nests) was greater than in remaining years combined (24.1% of 29 nests; $G = 3.84$, $P = 0.05$). Water levels were higher in 1988 than in the other years, and this was associated with larger Mallard clutches. Mean (±SD) clutch sizes in parasitized (10.9 ± 3.0, N = 11) and unparasitized nests (9.4 ± 2.0, N = 7) were similar in 1988 ($t = 1.08$, $P > 0.05$). Also, during the remaining years, clutch sizes in parasitized (7.8 ± 0.8, N = 5) and unparasitized nests (7.2 ± 1.9, N = 15) were similar ($t = 0.64$, $P > 0.05$).

TABLE 1
CHARACTERISTICS OF PARASITIZED AND UNPARASITIZED MALLARD NESTS

	Parasitized	Unparasitized
Fate		
Deserted	1[a]	4
Predated	6	5
Hatched	10	13
Clutch size	9.9 ± 2.9 (16)[b]	7.9 ± 2.2 (22)
Eggs outside nest	1.1 ± 1.9 (12)[c]	0.3 ± 0.8 (13)
Percent of eggs with dead embryo	10.5 (95)[d]	6.3 (95)
Percent of infertile eggs	8.4 (95)	3.2 (95)

[a] Number of nests.
[b] Mean ± SD (number of nests).
[c] Mallard eggs.
[d] Number of Mallard eggs in successful nests.

The mean number of Red-crested Pochard eggs in parasitized Mallard nests was 3.3 ± 1.3 (N = 16). On average, 0.6 ± 1.0 Red-crested Pochard eggs were displaced outside parasitized nests. Although more Mallard eggs were displaced outside the nest bowl in parasitized than in unparasitized nests, the difference was not significant (Table 1, $t = 1.61$, $P > 0.05$). The proportions of Mallard eggs with dead embryos were similar in parasitized and unparasitized successful nests (Table 1, $G = 1.10$, $P > 0.05$). Also, similar proportions of infertile Mallard eggs were found in both nest types (Table 1, $G = 2.50$, $P > 0.05$). However, when considering all factors that negatively affected hatching success (displacement outside the nest, breakage, infertility and dead embryo), fewer Mallard eggs hatched in parasitized (76.0% of 100) than in unparasitized nests (86.9% of 99; $G = 3.93$, $P < 0.05$).

Discussion.—In 1988 Mallard clutches were larger probably because of higher water levels (see Krapu et al. 1983). In addition, in this year there was greater proportion of Mallard nests parasitized by Red-crested Pochards. The clutch size of Mallards was larger in the parasitized than in unparasitized nests which I studied. However, when the data of 1988 were separated from the comparisons, there were no differences in clutch sizes between parasitized and unparasitized nests. In other studies in which laying dates between parasitized and unparasitized nests did not differ, clutch sizes were also similar in both types of nest (Heusmann et al. 1980, Amat 1985a). Talent et al. (1981) found larger clutches in unparasitized Mallard nests than in nests parasitized by Redheads, and following Weller's (1959) hypothesis, concluded that Redhead nest parasitism could have suppressed ovulation in Mallard hens. However, Talent et al. (1981) did not control for effect of laying date on clutch size; thus, their conclusion might be incorrect. Perhaps, the effects of nest parasitism on hosts have been overemphasized, because clutch sizes in parasitized nests may not have been reduced (Amat, unpubl. data). Factors known to cause variations in clutch sizes in waterfowl should therefore be controlled when making comparisons between parasitized and unparasitized nests, for the deposition of parasitic eggs can yet be implicated as an influence on reduced host clutches in parasitized nests.

In other studies it was found that the proportion of eggs with dead embryos was greater in parasitized than in unparasitized successful nests (Amat 1985a, Davies and Baggott 1989), but I did not observe this in the present study. The number of eggs deposited by Red-crested Pochards in Mallard nests was similar to that deposited by Redheads in nests of the same host species (Talent et al. 1981). When Red-crested Pochards and Redheads each parasitized

other duck species, the number of host eggs displaced outside the nest bowl was significantly greater in parasitized than in unparasitized nests (Weller 1959, Joyner 1976, Sugden 1980, Amat 1985a), but this was not evident when each parasitic species deposited their eggs in Mallard nests. However, as Talent et al. (1981) also found, egg success was lower in parasitized Mallard nests, which resulted from a combination of factors, of which egg displacement seemed to be the most important. As clutch size was not reduced, I conclude that the effects of Red-crested Pochard nest parasitism on Mallards, although adverse, were not as detrimental as Talent et al. (1981) implied when the same host species was parasitized by Redheads.

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Brown-headed Cowbirds parasitize Loggerhead Shrikes: first records for family Laniidae.—Friedmann et al. (1977) and Friedmann and Kiff (1985) report no instances of Loggerhead Shrikes (*Lanius ludovicianus*) rearing Brown-headed Cowbird (*Molothrus ater*) young. Furthermore, we can find no literature accounts of cowbird parasitism of North American members of the family Laniidae. The following observations therefore represent the first documented records of cowbird parasitism of Loggerhead Shrikes, as well as the first account of shrikes rearing cowbird young from eggs deposited by cowbirds. Two previous accounts of shrikes rearing blackbirds (*Agelaius* spp.) and Brown-headed Cowbirds have been reported, but in each case the foreign eggs were deposited by a researcher (Potter 1939, Rothstein 1982).

We monitored 261 Loggerhead Shrike nests initiated by 110 pairs in 1987–1989 in southwestern Iowa as part of a study of productivity and habitat preferences of shrikes nesting along roadsides. Most nests (N = 251) were located in roadside ditches; the other 10 nests were situated in fencerows and pastures away from roads. Shrikes initiated nests from 6 April through 11 June, with peak nesting in the second and third week of April.

During the study, we encountered three shrike nests parasitized by Brown-headed Cowbirds. On 2 May 1988, we found the broken shell of a cowbird egg in a shrike nest along a road in a mulberry tree (*Morus alba*). The nest had contained a clutch of six shrike eggs five days earlier. On 26 May, we found a clutch of five shrike eggs, which we estimate to have been completed two days earlier, in the same nest. The clutch hatched 14 days later and fledged without any further observed parasitism. Others have observed that cowbirds sometimes place eggs in empty nests (Friedmann 1929; Best, pers. obs.), and we suggest that when the first shrike clutch was lost to predation, the cowbird placed the egg in the temporarily deserted nest.

The second incidence of parasitism was discovered on 4 June 1988, at a roadside nest in a small boxelder (*Acer negundo*) shrub. The nest contained four, one-day-old shrike chicks and a single 7- or 8-day-old cowbird nestling (age estimates were based on body size and feather development; Friedmann 1929, Lohrer 1974). The age gap between the nestlings corresponded to the difference between the incubation periods of the two species (16–17 days for shrikes and 11–12 days for cowbirds; Bent 1950, Nice 1953), indicating that the cowbird had laid the egg before the onset of incubation. This nesting attempt was the third for the shrike pair that season, following two previous attempts that ended in predation. On 7 June, we revisited the nest and found three shrike nestlings and no cowbird. We assume that the cowbird chick fledged during the interval between visits, as most cowbirds fledge at 10 days of age (Friedmann 1929).

The third incidence of parasitism occurred on 16 April 1989. We discovered a clutch of three shrike eggs and one cowbird egg in a nest along the road in a roadside plum (*Prunus americana*) thicket, and by backdating from the hatch date, we estimated that incubation had begun three days earlier. Two shrike eggs hatched on 1 May, and the other shrike egg disappeared, but the cowbird egg failed to hatch and disappeared between our visits on 6 and 9 May. One shrike eventually fledged on 19 May. The other nestling had disappeared between the 9 May and 13 May visits.

Further evidence for cowbird parasitism of shrikes was suggested by the behavior of shrikes when their nest sites were approached by cowbirds. On two occasions at separate sites, we saw shrikes chase cowbirds that had approached their nests which contained eggs. Both instances occurred during the last week of April. Most shrike nests are less concealed early in the season. Thus, it may be more difficult for a cowbird to approach the nest without being detected. Many passerine species recognize cowbirds as a threat, and the level of

aggression directed towards cowbirds is positively correlated with the rate of their parasitism (Robertson and Norman 1976).

Reasons for lack of observed parasitism in shrikes are uncertain. Friedmann (1929, 1963) speculated that the shrike's freedom from "molothrine annoyance" was due to its aggressive and predatory nature. Shrikes typically prey upon insects, small rodents, and sparrow-sized birds (Bent 1950, Craig 1978, Kridelbaugh 1982), although cowbird-sized birds are taken on occasion (Bent 1950, Ingold and Ingold 1987). In addition, Rothstein (1982) determined that shrikes were egg rejectors, although in two of 21 artificially parasitized nests, they accepted easily distinguishable blackbird eggs. The incidence of parasitism in a rejector species, therefore, would be detected only on the few occasions when a bird accepts the cowbird eggs (Rothstein 1971). Thus, cowbird parasitism could be more common than indicated by the available data. Nevertheless, several incidences of parasitism have been reported for other aggressive rejector species (e.g., Eastern Kingbirds [*Tyrannus tyrannus*] and American Robins [*Turdus migratorius*]; Friedmann 1963, Rothstein 1975). A lack of cowbirds does not explain the lower rate of parasitism of shrike nests in our study. Frawley (1989) reported that 49% of passerine nests with complete clutches in six alfalfa fields within our study area were parasitized by cowbirds.

The scarcity of parasitism in shrikes might also be attributed to the lack of overlap between their nesting season and those of the cowbird's other passerine hosts in the upper Midwest. Both Loggerhead Shrikes and Brown-headed Cowbirds arrive in Iowa in late March and early April (Dinsmore et al. 1984). Shrike egg laying peaks in mid-April, 3–4 weeks before the peak nesting-period of many acceptor species (Frawley 1989). Two of the three instances of parasitism discovered in this study occurred in renesting attempts initiated late in the shrike's nesting season, and the egg laid in mid-April failed to hatch.

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Nests and eggs of some Costa Rican birds.—Although Costa Rica has a relatively well-studied avifauna, much remains to be learned about the breeding biology of many species. New breeding information for several species was collected in Costa Rica during 1984–1986 in a field survey conducted by the Western Foundation of Vertebrate Zoology (WFVZ). In this paper, we include information on seven species for which the nest and/or eggs previously were undescribed, although a summary of this information appeared in Stiles and Skutch (1989). Nomenclature follows that of Stiles and Skutch (1989), and egg shapes are those given by Preston (in Palmer 1962).

Vermiculated Screech-Owl (*Otus guatemalae*). Two vague references have been made to the breeding of this species. On 11 April (1942 ?), Sutton and Pettingill (1942) collected a female with enlarged ovaries in southwestern Tamaulipas, Mexico, at the entrance to a nest. The cavity was 15 ft (4.5 m) from the ground, but the nest contents were not determined. Wetmore (1968) reported a female collected on 19 March 1949 near Utive, Panama, with a nearly shelled egg in the oviduct. On 3 April 1986, while working at Cerro Montezuma (700 m), Alajuela Prov., about 45 km NE of Las Cañas, we flushed and collected a female (WFVZ #36,871) from a nest. The nest site was located in disturbed forest and was situated in a cavity in a decaying stump about 5 m from the ground. The cavity was 5 cm deep, and the entrance measured 23 × 18 cm. The shallow depth of the cavity suggested that it was made by a trogon rather than by a woodpecker. The nest contained two eggs deposited directly on wood chips. The slightly incubated eggs (WFVZ #154,790) are unmarked white, slightly glossy, and spherical, and they measure 35.10 × 30.51 and 34.30 × 29.60 mm.

Andean Pygmy-Owl (*Glaucidium jardinii*). We discovered a nest of this species on 26 March 1986 at an elev. of about 2000 m on the western slopes of Volcán Barva at La Concordia, Heredia Prov., about 24 km NW of San José. The nest site was located on a ridge at the edge of disturbed forest and pasture land with scattered stumps and mature trees. Our attention was drawn to the vicinity of the nest site by two loudly vocalizing Emerald Toucanets (*Aulacorhynchus prasinus*), which were being attacked by one of the

pygmy-owls that flew toward the toucanets from a small hole in a stump. The pygmy-owl was immediately collected (WFVZ #36,877), and it proved to be a female. The nest cavity was an abandoned woodpecker nest probably made by a woodpecker (*Melanerpes* sp.). The entrance was located 2.1 m from the ground. The 45-cm deep cavity contained three slightly incubated eggs (WFVZ #154,767) deposited on a bed of wood chips. The eggs were white, not glossy, and short subelliptical (2) and spherical (1) in shape, and they measured 29.57 × 24.62, 29.33 × 24.54, and 28.15 × 24.67 mm.

Dusky Nightjar (*Caprimulgus saturatus*). On 13 March 1986, at Hacienda San Miguel (ca 2050 m), 1 km E of Rancho Redondo, San José Prov., we were shown a nest of this species by an employee of the hacienda who had found it a few days earlier when he flushed the incubating bird. By the time of our arrival the nest was abandoned, apparently the result of predation, as most of the female's tail feathers were found on and adjacent to the nest. The single egg was intact (WFVZ #154,755) and contained a large dead embryo. The nest was located on a natural terrace, which was partially covered by tall grass and ferns, with some clearings and a few large trees. The nest was a small grass-lined depression about 10 cm in diam. The single egg was white, slightly glossy, and measured 28.65 × 21.62 mm.

Snowcap (*Microchera albocoronata*). MM discovered a nest of this species on 17 April 1986 at Finca Plastico ("Rara Avis"), Horquetas, about 29 km NW of Guapiles (650 m), Heredia Prov. The nest was located in the understory of primary forest on a slope leading toward a small creek. It was placed about 1.6 m from the ground at the base of a leaf on the outer branch of a small plant. The cup-shaped nest was made with brown moss mixed with green moss and lichens, and the lining contained brown moss and lichens. The female was secured (WFVZ #38,841). The two eggs (WFVZ #154,786) contained large embryos. They were dull white, long elliptical and subelliptical in shape, and measured 12.45 × 7.95 and 12.02 × 7.98 mm, respectively. Earlier, Carriker (1910) mentioned a nest collected in March 1908 above Guapiles. He described the nest as "a tiny little thing, built on a small knot on the side of a slender vine, hanging from a large tree." The eggs were broken when he attempted to collect them. F. G. Stiles (pers. comm.) encountered a nest of this species with two newly hatched young at "Rancho Levi," a small grassy clearing surrounded by forest (ca 720 m), about 3 km SE of Finca Plastico, on 3 April 1985. The nest was 1.75 m up in the lowest branches of a tree overhanging the edge of the clearing. It was rusty-brown in color, composed of tree fern scales, fine fibers and spiderwebs, and decorated with green moss and a few bits of lichen on the exterior.

Black-cheeked Woodpecker (*Melanerpes pucherani*). Several nests of this species have been reported, but the eggs are apparently undescribed. Stone (1918) mentioned a nest hole in a dead tree in a clearing on 4 April 1911 in Gatún, Panama. Russell (1964) reported five nests found in Belize between the months of April and July which were placed between 12 to 55 ft (3.65 to 16.75 m) above the ground in palms or dead trees. Skutch (1969) made observations at a nest in Costa Rica during April and May 1941. When he observed the male ejecting an egg, he examined its remains, which appeared small for this species. He suggested that woodpeckers remove from their own nests any small or visibly abnormal eggs. On 14 May 1986, at Zapote, Bijagua (500 m), Alajuela Prov., about 45 km NE of Las Cañas, we collected a set of two fresh eggs (WFVZ #154,781). Interestingly, one of the eggs seems to be abnormally small, as Skutch (1969) reported for the eggshell remains he examined. The eggs were glossy white, and they measured 24.71 × 16.33 and 21.24 × 15.32 mm. They were subelliptical and short oval in shape, respectively. The nest was located in a hole in a stump in a pasture about 8 m from the ground. The cavity was 35 cm deep, and the diameter of the entrance measured 10 × 8 cm. The nest contained one egg when checked on 12 May. Based on the contents of two other nests examined, two eggs may comprise a complete clutch. A second nest found on 12 May 1986 in a nearby pasture was 3.5 m above

the ground and contained two well-grown chicks. A third nest examined on 3 May at Cerro Montezuma was located 6 m up in a stump at the edge of pasture and disturbed riparian forest. It contained four recently hatched chicks that were unfeathered and flesh colored. Thus, the clutch size for this species may range from 2–4 eggs.

Rufous-winged Tanager (*Tangara lavinia*). On 11 May 1986, at El Macho, Alajuela Prov., ca 45 km NE of Las Cañas at an elev. of 550 m, MM flushed one of these tanagers from a small citrus tree at the edge of a pasture near disturbed forest. Upon investigation, an almost finished nest was found. On 15 May, the bird was found on the completed nest, but no egg had yet been laid. On the 18th, the nest contained two fresh eggs (WFVZ #154,830) that were bluish-white in color and marked over their entire surface with spots of lilac, brown, purplish brown, and dark brown concentrated at the larger end. They measured 21.70 × 16.05 and 22.25 × 15.96 mm and were oval and subelliptical in shape, respectively. The nest was located in the outer part of a citrus tree about 1.6 m from the ground. It was cup-shaped and made with fine grasses mixed with some mosses, some dry leaves, and small roots and lined with fine blackish rootlets. Previously, Hilty and Brown (1986) mentioned a bird building a nest in July, W Valle, Colombia.

Black-and-yellow Tanager (*Chrysothlypis chrysomelas*). In a recent comprehensive review, Isler and Isler (1987) mentioned that there is no published information on the breeding of this species. On 22 June 1986, at Virgen del Socorro, Alajuela Prov., MM and F. Stiles observed a female entering a nest placed in the fork of an outer branch about 8 m up in an *Inga* tree within disturbed riparian forest. The nest (WFVZ #54,753) was cup-shaped and made with brown vegetable fibers, mosses, and dry leaves and lined with black vegetable fibers and fungal rhizomorphs. Unfortunately, the contents were lost during the collecting episode, which took place during a rainstorm. The female's insistence upon returning to the nest suggested that it contained either heavily incubated eggs or recently hatched chicks. The adult female was collected (WFVZ #35,513).

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A case of polygyny in the Wood Thrush.—Harem polygyny is rare among North American passerines as a regular breeding strategy, but it is not unusual as a facultative or opportunistic strategy (Ford, Current Ornithology 1:329–356, 1983). A single case observed during a long-term study of a color-banded population of Wood Thrushes (*Hylocichla mustelina*) indicates that this species may be listed among those rarely practicing harem polygyny.

From 1974–1990, Roth and co-workers observed 157 male Wood Thrushes (311 bird-years) and 719 nests in a Delaware woodlot (unpubl. data; see Johnson et al., Condor 92: 89–96, 1990 for site description and methods). At 30% of the nests, the male owner was identified positively, i.e., seen feeding the young or guarding the nest. We could clearly associate an identifiable male with most other nests, using capture data or observations of singing or scolding nearby. We cannot be certain that undetected harem polygyny has not occurred, but only this one case has been confirmed.

In 1990, we observed a male (Y) and a female (X1) nesting for their second year on our study site. Both had been mated monogamously in 1989. A predator destroyed the pair's first nest on 16 May 1990. X1 laid three eggs in a new nest 23–25 May; two young fledged 18 June. Y was identified as the male owner when Johnson saw him perched on this nest 3 June. A secondary female, X2, was initially seen by Bartlett on 31 May building a nest about 50 m from X1's. Y was netted 6 June within 25 m of X2's nest, but no male owner was confirmed there until Johnson saw Y feeding the nestlings on 20 June. The next day Bartlett observed Y again feeding X2's nestlings, and Bartlett and Johnson simultaneously saw him feeding one of X1's fledglings less than 1 m from X2's nest. Y was captured and given a new color-band combination on 22 June. On 25 June, Kleiner saw him feeding the nestlings at X2's nest, and Johnson saw him feeding a fledgling from X1's nest about 20 m from X2's nest.

One young fledged from X2's nest on 28 June. Johnson saw X2 foraging in the company of Y on 11 July. Another nest, built in early July near her first nest, probably was hers also. It failed 18 July, and X2 was not seen again. X1 built another nest in late June, and three young fledged from it 25 July, having been fed in the nest by Y.

Ford (op. cit.) suggested cases of harem polygyny in normally monogamous species may arise when a mated male acquires the territory and mate of a vanished neighbor. Such was not the case here; no other territorial male was in the area of X2's nests. Among regularly polygynous species, factors associated with polygyny include high male density with variation in territory quality (Verner, Evolution 18:252–261, 1964) and variation in male quality (Weatherhead and Robertson, Am. Nat. 113:201–208, 1979). We cannot judge which of these was important here; in 1990 male density at the site was at its highest level since 1977 (Roth and Johnson, in prep.), but we did not assess territory quality or male quality. Y's territory was in an area used annually by Wood Thrushes but was not clearly unusual. Y

did have relatively high reproductive success: only eight of the 28 other males on the site had equal or greater fledgling production.

The primary female, X1, did not noticeably suffer as a result of the secondary mating: only eight of the 29 other females produced more fledglings than she. X2's one fledgling exceeded only four others. Observers at X2's nest noted that Y fed those young very infrequently. This may have contributed to X2's poor success and may indicate one reason Wood Thrush females do not mate polygynously more often.

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Double-toothed Kites following tamarins.—There are several reports of birds using ants, other birds, and mammals as "beaters" that move through the vegetation flushing prey (Curio 1976). In the Neotropics, birds are frequently observed following groups of primates, mainly of squirrel monkeys (*Saimiri* sp.) and capuchins (*Cebus* sp.) (Moynihan 1970, Klein and Klein 1973, Fontaine 1980, Terborgh 1983, Boinski and Scott 1988).

Here I report on Double-toothed Kites (*Harpagus bidentatus*) following a group of pied bare-face tamarins (*Saguinus bicolor bicolor,* Callitrichidae) observed during an 11-month field study on the ecology of this primate (Egler 1986) in a disturbed forest near Manaus, Amazonas State, Brazil.

The Double-toothed Kite occurs from southern Mexico to eastern Bolivia and southeastern Brazil (Brown and Amadon 1968, Sick 1985). It preys mainly upon large arthropods, frogs, lizards, and bats (Schubart et al. 1965, Brown and Amadon 1968, Ridgely 1976, Fontaine 1980, Wetmore 1981, Boinski and Timm 1985, Boinski and Scott 1988).

Observations were made from May 1983 to April 1984, except for October 1983, in a 20-ha study area on the left bank of the Rio Negro near the mouth of Tarumã-açu stream (3°8′S; 60°2′W, elev. 40 m). A trail system divided the area into 50 × 50-m quadrats (Egler 1986). Tamarins were studied during 46 observation days (06:00–17:00 h) with a mean of four days per month. Instantaneous scan sampling (Altmann 1974, Clutton-Brock 1974) was used with five-minute intervals to quantify tamarin behavior. I divided tamarin behavior into four categories: (1) resting, (2) traveling, (3) feeding on plant material, and (4) foraging for animal prey. The presence of Double-toothed Kites was recorded only when observed simultaneously with tamarins. Durations of following periods were calculated by summing the five-minute intervals during which kites were observed following tamarins. When subsequent observations were within 25 min of each other, intervals between observations were also included in the calculations below. On these occasions (e.g., when tamarins were resting), it was difficult to observe the kites within the foliage, but with further movements by the tamarins, they became visible again. Distances travelled by kites were calculated by running a curvimeter on tamarin routes drawn on a map of the study area (scale 1:2500). Eleven observations of only one five-min. interval were excluded because I could not determine a distance during these observations.

I obtained a total of 4607 samplings (ca 120 samplings/day) of tamarins among which in 721 (15.6%) I observed Double-toothed Kites following them. Two individual kites were observed simultaneously in 55 samplings. Among the 721 samplings with kites observed, 56.2% were when tamarins were traveling, 22.3% when resting, 14.3% when foraging for animal prey, and 7.2% when feeding on plant material. These frequencies were not significantly different from the frequencies of tamarin activity ($\chi^2 = 1{,}26$, df = 3, $P > 0.5$).

During periods when tamarins were traveling, kites were observed flying at heights similar to, or below, those occupied by tamarins. When tamarins rested within tangles of lianas or on branches, kites perched near them until the group moved again. On three of these occasions, the kites flew very close to the resting tamarins; on two occasions, the kites touched a resting tamarin with their claws while hovering. This behavior elicited reaction only by the touched tamarin who was trying to shake off the kite's claws without moving away from its resting place. I never observed tamarins mobbing Double-toothed Kites, although they mobbed a perching White Hawk (*Leucopternis albicollis*) and an opossum (*Didelphis* sp.) that was moving within the canopy.

On only three occasions, I observed kites capturing prey, all of them large cicads in flight, probably flushed by the tamarins. Kites flew toward the cicads, catching them on the wing with their claws and then perching to eat the prey.

Kites were observed following tamarins throughout the day with no marked difference between morning and afternoon hours. Periods during which kites followed tamarins varied from two to 57 five-min intervals. During nearly two-thirds of the observations, kites followed tamarins for short periods, ca 1–10% of complete observation days, moving small distances of less than 400 m. In only six occasions kites followed tamarins for long periods (25.0–47.5% of complete observation days) and moved long distances of 825–1512 m.

The frequencies of Double-toothed Kites following pied bare-face tamarins observed in this study are similar to those observed by Boinski and Scott (1988) and Fontaine (1980) in capuchin and squirrel monkey studies, although methods for calculating these frequencies were different.

The relationship between Double-toothed Kites and primates may be regarded as commensalistic (Boinski and Scott 1988). By following primate groups kites have access to prey otherwise inaccessible or barely accessible (Boinski and Timm 1985, Boinski and Scott 1988), thus enhancing their feeding efficiency. Supporting the latter suggestion, Boinski and Scott (1988) observed that birds followed monkeys more frequently during periods of arthropod scarcity. Among primates, Double-toothed Kites tend to follow more frequently those species that have higher activity levels and include arthropods in their diet (see Fontaine 1980). Tamarins are highly active and insectivorous (e.g., Terborgh 1983, Egler 1986) which would contribute to their effectiveness as beaters for these kites.

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Unprecedented stopover site fidelity in a Tennessee Warbler.—The postbreeding movements of long-distance migrant passerines are not well understood. Here we report the recurrence of an adult male Tennessee Warbler (*Vermivora peregrina*) during three successive autumns at a stopover site in the St. Croix River valley in east-central Minnesota (Washington Co., approximately 44°55′N, 92°48′W). This site is at least 240 km south of the nearest recorded or suspected breeding grounds (Janssen 1987; D. F. Parmelee, pers. comm.).

Migrant passerines showing stopover site fidelity are rare in the literature. Nisbet (1969) published a call to banders for records of transient migrants that returned to the site of banding in subsequent years. He arbitrarily designated "good" transients as those individuals occurring more than 100 mi. (161 km) from the species' regular breeding or wintering ranges. He received eight convincing records from his request. Since Nisbet's review, the number of "good" transients appearing in the literature has not increased dramatically; we counted records of approximately 21 individuals of 10 species (Nisbet 1969, Ryan 1970, Woodward 1972, Johnson and Ellis 1974, Leberman and Clench 1975, Foy 1975, Ely and Weber 1977, Goodpasture 1979).

During the spring (May) and autumn (mid-August through late-September) migration periods of 1984–1986, we captured migrants in five wooded habitat types using standard 30 mm and 36 mm mesh nylon mist nets (12 × 2.5 m). We accumulated over 70,000 net-h in three spring seasons, and over 65,000 net-h in the corresponding autumns. Nets were oriented E-W and spaced 30 m apart; net locations remained the same throughout the study (see Winker et al., in press for more detail).

Recaptures between years at our site were possible only for birds first captured in 1984 or 1985. Considering only these years, spring effort was 43,428 net-h (20 Tennessee Warbler captures), and autumn effort was 47,970 net-h (552 Tennessee Warbler captures). On 23 August 1984, we captured an individual (TEWA 1700-35375) with a fully ossified skull that was sexed as male, using the criteria of Raveling and Warner (1965). This same individual was subsequently recaptured seven times: three more times in 1984 (25 August, 5 and 9 September), and a total of four times in the next two autumns (19 and 23 August 1985, 25 August and 12 September 1986). All captures occurred at three adjacent net sites, and spanned a linear distance of only 60 m in an alder (*Alnus rugosa*) swamp bordering a small deciduous broadleaf woodland. In 1984, the recapture period spanned 17 days, and the bird experienced a net change in mass of −0.1 g. In 1985, the recapture period was only four days, with a net mass change of −0.2 g, and in 1986 mass change was 0.4 g in an 18-day period. In each season, the bird was molting, as were many autumn adults of this species at our site. Of 128 autumn adults for which molt was assessed, 72 (ca 56%) showed some molt, and 32 (25%) were molting extensively. The latter individuals were almost invariably molting in the alar and/or caudal tracts, and the recurring individual was a member of this category.

Following each capture, TEWA 1700-35375 was moved for measuring to a central location 130–190 m from the capture site. The release point was surrounded by woodlands in which the species regularly occurred, but this habitat was of a different type than the capture locale. The bird's subsequent return to the area and specific habitat of capture suggests that an attraction to this specific location existed within a season as well as between years.

This Tennessee Warbler is unique among the published list of "good" transient recurrences for several reasons. It is the only individual to return in three successive years; it is the only one recaptured more than once within a season; and it is apparently the only one which underwent prebasic molt at the site of capture. Nisbet (1969) hypothesized that the birds he reviewed had returned to presumably favorable sites to replenish fat reserves. The Tennessee Warbler returning to our site did not seem to be depositing fat.

We draw three conclusions from the evidence considered here: (1) site fixation (resulting in site fidelity) in transient passerines can occur at stopover sites but seems to be rare; (2) northerly stopover sites provide resources both for completion of the prebasic molt and for continued migration; and (3) the presence of adults in molt far from their regular breeding grounds and in samples collected in a TV tower kill (Raveling 1963:13) suggests that Tennessee Warblers can show an overlap of nocturnal migration and prebasic molt.

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The response of adult Red-cockaded Woodpeckers to a fallen nestling.—On 31 May 1990, while watching a pair of Red-cockaded Woodpeckers (*Picoides borealis*) feeding two 20-day-old nestlings, we observed the following behavior. At 6:30 DST, the adult male flew to the entrance of the nest cavity with prey. He did not immediately offer the prey to the nestlings, but hesitated at the entrance for several seconds. One of the nestlings lunged forward, apparently to snatch the prey from the adult, only to lose its balance and fall from the 12-m-high cavity to the ground where it remained out of sight near the base of the cavity tree. Both adults continued to feed the nestling still in the cavity, but did not approach the one on the ground, even though it called periodically. After ca 1.5 h, the adult female flew to the base of a pine (1 m from the base of the nest tree), positioning herself 0.5 m above the ground. She called continuously to the fallen nestling, which replied. The adult then flew to the base of the nest tree, again staying 0.5 m above the ground. I could not see the nestling, but I could hear it calling constantly. The adult began to hitch up the bole of the nest tree while continuing to call. The nestling came into view clumsily hitching up the bole behind the adult. The adult frequently looked back at the young bird and stopped periodically. After climbing to ca 4 m above the ground, the nestling lost its foothold and fell again. The adult immediately flew down to the base of the tree and the process was repeated. After four such episodes, the adult flew off. We interpret this adult behavior as attempts to guide the nestling up the tree. While the adults were away, the nestling hitched about 1.5 m up the nest tree and stayed there for 1.5 h. It gave begging calls each time an adult flew to the nest cavity, but it was never fed. The adults fed only the nestling that remained in the cavity.

After completing 3 h of feeding observations, we obtained five cerambycid larvae (southern pine sawyer, *Monochamus titillator*) from some pine slash (tree tops and major branches lying on the ground) left over from a thinning operation and fed them to the fallen nestling. The adult male had been observed obtaining larvae by foraging on the logging slash.

We returned one hour later to find the nestling in the same spot. Soon an adult (sex

unknown) flew to the nestling and fed it. Again, the adult appeared to guide the young bird up the bole. At 4 m, the nestling stopped. The adult hitched up the bole a few meters in front of the nestling and then flew back down to it, calling all the while. After repeating this several times, without the nestling moving further, the adult flew off. Shortly thereafter, we placed the nestling back in the nest cavity. Both nestlings fledged a few days later.

The adult behavior may have served one of two functions. It is possible that the adults were attempting to guide the fallen nestling back to the cavity, suggesting the adults somehow sensed that it was too soon for normal fledging. Perhaps Red-cockaded Woodpecker nestlings falling from cavities occurs with enough frequency to have selected for such adult behavior. Alternatively, the adults may have been attempting to guide the young bird to cover in the crown of the tree. The use of various calls and motions is common parental behavior among birds and serves to encourage their young to follow them to safety. Unfortunately, the fallen nestling never reached cavity height.

Our observation of a male Red-cockaded Woodpecker feeding on pine logging slash is relatively unique. Red-cockaded Woodpeckers forage mainly on live pines, to a much lesser extent on pines that have died recently, and on hardwoods (Hooper and Lennartz, Auk 98: 321–324, 1981; Porter and Labisky, J. Wildl. Manage. 50:239–247, 1986). To our knowledge, there are very few reports in the literature of Red-cockaded Woodpeckers feeding on pine slash (Ligon, Auk 87:255–278, 1970; Hooper and Lennartz 1981). We have also observed Red-cockaded Woodpeckers foraging on windthrown pines on two occasions. If Red-cockaded Woodpeckers feed regularly on slash left during cuts made to treat southern pine beetle infestations, insecticides sprayed on slash during some treatments (Swain and Remion, USDA Agric. Handb. 575, 15 pp., 1981) could be harmful to the woodpeckers.

Acknowledgments.—We thank J. Walters, J. Jackson, and F. James for constructive comments on an earlier draft of this note.—Richard R. Schaefer, D. Craig Rudolph, and Richard N. Conner, *Wildlife Habitat and Silviculture Laboratory, Southern Forest Experiment Station, USDA Forest Service, Nacogdoches, Texas 75962.* *Received 5 Feb. 1991, accepted 1 April 1991.*

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Learned song variations in British Storm-Petrels?—The occurrence of dialects in the songs of Oscine songbirds is well known (e.g., Baker and Cunningham 1985) and usually is attributed to the prevalence of song learning among those species (Lemon 1975, Slater 1989). Vocal learning has been described in several other avian groups (e.g., Baptista and Schuchmann 1990, Sparling 1979) but not in the Procellariformes. It is, therefore, interesting that James (1985) has found geographical variation in calls of the Manx Shearwater (*Puffinus puffinus*) and also in the purring song that male British Storm-Petrels (*Hydrobates pelagicus*) produce in their nesting crevices during the breeding season. This song or purr-call consists of a rapid trill of brief clicks (the purr), followed by a flourish of wide frequency band noise, known as the breath-note. The purr is rather over 1 sec in length, and the breath-note lasts about 0.25 sec; a series of songs is produced in quick succession with only 0.01–0.03 sec between them. James found significant differences among four sites in the click rate within the purr, in breath-note length, and in the gap between songs. The most marked differences were between birds recorded on Puffin Island, S.W. Ireland, and Mousa in the Shetland Islands, N. of Scotland, two sites some 1100 km apart.

If these geographical variations stem from learning, we might also expect to find microgeographic variation in the song, as is usual in Oscines. For example, territorial songbirds

often learn from their neighbors so that birds on adjacent territories have songs more similar than those farther apart (see Slater 1989 for a review). Features of song might also change with time. James (1985) found various aspects of Manx Shearwater calls to change in this way, but he could find no evidence for microgeographic variation in that species. Here I report on the results of recordings aimed at examining whether local differences in song could be found in storm-petrels and whether there is evidence for temporal variation.

The results are based on recordings of 37 individuals made on Mousa during August 1986. Recordings were made at 19 cm/sec with a Nagra IV-S tape recorder, between 23:00 and 01:00 h BST, the time when most song occurs. The microphone used was that of a QMC ultrasound detector as another aim of the research was to test whether petrels echolocate (Ranft and Slater 1987). Subsequent analysis was carried out using a Kay Digital Sonagraph 7800 with wide band setting, using one sonagram from each individual. Cadence (time from start of one song to start of next), breath-note length, and click rate within the purr were the main measures taken from these. Purr rate slowed during the song in all 37 birds. To allow for this, the measure used was the mean of that for a 0.5-sec period at the start and another just before the breath-note. The petrels recorded were nesting in dry stone walls so that their positions were arrayed along a single dimension and could be simply ranked in relation to each other. Two walls were examined, with recordings of 19 birds in one and 18 in the other. The sites were 550 m apart.

Click rate did not vary much among the birds (coefficient of variation [CV] = 5.3%), but the other measures varied more substantially (e.g., cadence, CV = 14.2%; breath-note length, CV = 12.6%; purr length, CV = 15.5%). Click rate did not correlate with purr length ($r = -0.096$), but the length of the purr and that of the breath-note were strongly correlated ($r = 0.581$, $P < 0.001$), showing that long songs tend to be long in both their main components. However, no evidence was found for any systematic variation in song within Mousa for any of the three measurements. There was no difference between the two sites on any of them (Mann-Whitney *U*-tests, $P > 0.10$), nor did birds with similar values nest closer together ($P > 0.05$). This was tested by scoring the value for each bird as being either above or below the median of all measurements and carrying out a runs test (Siegel 1956) to see whether high and low values tended to occur in series. While the breath-note of most birds had no clear structure, in 13 individuals there was a brief tonal section at its onset. Again a runs test was used to see if there was any evidence that these were clustered, but no significant effect was found ($P = 0.15$). Thus, although there was considerable variation among the birds, there was no suggestion that this was other than random in distribution.

These results have failed to find any microgeographic variation in storm-petrel song such as might be expected if song were learned from neighbors. It remains possible that it is learned before birds settle to nest and that they do so at random in relation to the songs of those round about them, an explanation also proposed by James for the lack of microgeographic variation in Manx Shearwater calls. On the other hand, as the storm-petrel sites examined by James (1985) are very distant from each other, another possible explanation for his results on this species is that the populations involved are almost totally isolated from each other so that the geographical differences have arisen without the involvement of learning. In Northern Bobwhite (*Colinus virginianus*), differences in the separation call sufficient to allow recognition of covey mates have arisen without the involvement of learning (Baker and Bailey 1987).

Changes in calls with time, such as James (1985) found in Manx Shearwaters, are also most likely to arise through vocal learning. A comparison with his data, collected in 1983, suggests that such changes may occur in storm-petrel calls as well. The mean purr rate found here was 8% lower than he reported for Mousa (38.1 vs 41.3 elements/sec: 2/35 birds recorded

here showed higher rate than the latter mean, sign test $P < 0.001$), while mean song length was much higher (1.51 vs 1.31 sec: 8/35 lower, $P < 0.002$), as were breath-note length (0.24 vs 0.20 sec: 0/35 lower, $P < 0.001$) and the gap between songs (0.03 vs 0.01 sec: 2/35 lower, $P < 0.001$). My results are closer to those at his other sites than are those from his Mousa recordings on the measures that he found significantly different.

These results suggest that storm-petrel song does change with time, but it is necessary to be cautious. Such substantial changes over only three years seem unlikely and it is possible that they are accounted for by differences in equipment. The recordings from Mousa that James used for his analysis were made with much less sophisticated equipment than that used here and that which he used elsewhere. Very slight differences between recording and playback speeds on such equipment could lead to significant differences from other results. Thus the extent to which petrel songs show temporal variation must remain an open question, but it is certainly one which deserves further investigation. Geographic variation certainly does exist in storm-petrels, as James (in litt.) found significant differences among his other three sites, at all of which the same equipment was used for recording. The results reported here suggest that, as with Manx Shearwaters, this variation is not accompanied by micro-geographic differences within the breeding population.

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Tristram's grackles groom Nubian ibex.—There are relatively few species of birds that have been observed actively grooming cattle or other large animals, although Cattle Egrets (*Bubulcus ibis*) do occasionally perch on large herbivores and pluck insects from their hides (Heatwole 1965). Examples in Africa include the association between the Egyptian Plover (*Pluvianus aegyptius*) that has been observed to walk into the open jaws of the Nile crocodile and to glean food particles from between its teeth (Howell 1979). In the Galapagos Islands, one of Darwin's finches (*Geospiza fuliqinosa*) removes parasites from the hides of marine iguanas (*Amblyrynchus cristatus*) (Amadon 1967). In sub-Saharan Africa, oxpeckers (*Buphagus* sp.) clean ectoparasites from the hides of zebra (*Equidae* sp.), giraffe (*Giraffa* sp.), impala (*Aepyceros melampus*) and cape buffalo (*Syncerus c. caffer*) (Breitwisch, pers. comm.). Individuals of the species always accompany large herds of animals and derive a large part of their diet from eating ectoparasites which they pick from their host's bodies (Mackworth-Praed and Grant 1955, Breitwisch, pers. comm.). In the United States, Scrub Jays (*Aphelocoma coerulescens*) which accompany black-tailed deer (*Odocoileus hemionus columbianus*) have been observed maintaining "grooming stations" (Isenhart and DeSante 1985). The phenomenon of "grooming stations" is very similar to that known to exist in fishes in coral reef communities (Fishelzon 1983).

In most cases, both parties profit. The cleaning individual is protected from predators and has a regular food resource at its disposal. The larger animal benefits by having otherwise unreachable parasites and other nuisances removed. It should be noted that oxpeckers have been observed pecking at wounds on their hosts. This behavior has been interpreted as keeping the wound unhealed and thus attracting flies and other insects which are then picked off by the oxpeckers. They have also been observed to tear off fragments of flesh and skin (Breitwisch, pers. comm.).

In Israel, along the western bank of the Great Rift valley (on the shores of the Dead Sea) is a spring called Ein-Gedi. To the north of it is Mount Yishay, on which an artificial basin was dug by the Nature Reserves Authority to collect water flowing from several tiny springs. This pool attracts a wide range of animals at all hours of the day and night. A toothbrush tree (*Salvadora persica*) serves as a perch for a flock of Tristram's grackles (*Onycognathus tristramii*) which can be found perching in this tree in the early morning. Tristram's Grackle resembles the Blackbird (*Turdus merula*) in size. Only Tristram's grackle has moved beyond the bounds of the African continent and has a limited distribution in Aden, Yemen, along the shores of western Saudi Arabia, eastern Sinai, and up the Rift valley as far north as Jericho (Paz 1986). It is gregarious at most times and usually is found in small groups comprised of parents and offspring. In winter, it forms flocks of 100–300 individuals (Paz 1987).

We started regular observations of the grackles' interactions with Nubian ibexes (*Capra ibex nubiana*) after a chance sighting, by RY, early one morning in mid-April 1988. We noticed that an approaching herd of ibexes elicited from the birds a greater cacophony of noise than is usual and that the grackles started hopping on the branches of the tree.

Upon arrival of the herd, an ibex would remain stationary and a single Tristram's Grackle would fly to it and land on its back. After an initial, mutual exchange of gestures—bowing and cooing by the bird and neck stretching by the ibex—the bird would move up toward the head area. Only then would it start to groom and peck at the hide of the ibex.

During two years, we visited the area at dawn on 17 occasions and observed grackle–ibex interactions on 14 of these. The average grackle flock size during our 17 visits was 28.8 $\pm$ 9.9 (SD). Ten visits were between the winter (non-breeding) months of September to March. The average flock size for these months was 36.3 $\pm$ 4.4. Seven visits occurred between the

summer (breeding) months of April and August and the average flock size was 18.0 ± 2.4. As implied from these data, flock size was larger during winter (Mann-Whitney *U*-test, $U_{7,10} = 70$, $P < 0.005$). We assume that during summer pairs were busy with nesting and that only juvenile or unpaired individuals were present at the station. During winter, the addition of all breeding adults and young from the previous breeding season accounted for the rise in flock size. Other possible explanations for changes in flock size over season may include migratory behavior or increased dependence on ibexes when other sources of food are scarce in winter.

The birds seemed to be capable of identifying herds of ibexes at distances of over 100 m. The approach of a herd caused them to whistle louder and more intensely and to hop about excitedly in the bush or tree.

The cleaning process usually began around the eyes, the ears, and even the horns. The ibexes assisted the grackles by stretching or moving appendages as needed. The grackles gave particular attention to the ears and the area adjacent to the sexual organs. Although we could not identify each individual, we noted that there was an idiosyncratic system characteristic of each bird in the manner in which it cleaned an ibex.

In all 74 instances of grackle–ibex interactions, the birds cleaned in the same direction: from the head toward the tail of the ibex. In all instances, only one bird at a time was seen to clean an ibex. No aggression or competition for the cleaning of an ibex was observed. It is of interest to note that the ibexes cleaned were either juvenile males or females. Adult males and kids were not gleaned, and they would usually graze in the immediate vicinity, waiting for the other members of the herd to finish being cleaned before continuing on their way.

By means of local publications, we requested information and pictures of such chance observations. Twenty-six people responded to our request, 17 of whom reported on grackles cleaning ibexes, two of Fan-tailed Ravens (*Corvus rhipidurus*) perched on ibexes, and three of Hooded Wheatears (*Oenanthe monacha*) in the company of ibexes. This concurs with previous descriptions by Aharonson (1982) and Paz (1986). Four reports were from nomadic bedouin who reported the exact locations in which their camel herds go to get themselves cleaned by Tristram's Grackles.

This phenomenon of bird–mammal interactions still needs to be studied in detail and to be quantified. The study does raise questions about foraging patterns, symbiotic relationships, and individual recognition patterns. We are convinced that this interspecific behavior is more widespread than is appreciated and is only waiting to be discovered by ethologists.

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Two new host species for the parasitic blow fly *Protocalliphora braueri*.—Larvae of the parasitic bird blow fly *Protocalliphora braueri* (Diptera: Calliphoridae) are reported from two new host species, Brewer's Sparrows (*Spizella breweri*) and Sage Thrashers (*Oreoscoptes montanus*). Larvae were found on 57 nestlings in south central Idaho, 32 km north of Shoshone in Blaine county. The habitat in this area is dominated by big sagebrush (*Artemisia tridentata*) and a variety of grasses. Both bird species are sagebrush obligates (Braun et al. 1976) and are widely distributed throughout the shrub-steppe region of western North America during the nesting season (Wiens and Rotenberry 1981).

Protocalliphora braueri, a widespread species (synonym is *P. hirundo*), has been recorded attacking several North American bird species (Garrison et al. 1986, Halstead 1988, Eastman et al. 1989, Gold and Dahlsten 1989, Sabrosky et al. 1989). It is believed that the flies overwinter as adults and take advantage of early nesters. It is not known whether female flies oviposit in the nest material or directly on the nestlings (Sabrosky et al. 1989). Unlike most *Protocalliphora* larvae which live in nest material and feed intermittently on their hosts, *P. braueri* larvae produce myiasis by burrowing into the subcutaneous tissue of their host. They are hematophagous and require from one to three blood meals to mature. The myiasis-producing habit of *P. braueri* can lead to substantial host tissue damage. The larvae have been reported to burrow into the brain and pleural cavities of hosts (Sabrosky et al. 1989).

Brewer's Sparrows were infrequently parasitized by *P. braueri,* and I recorded larvae in only 4 of 68 (6%) nests. Sage Thrashers were more frequent blow fly hosts with 15 of 40 (38%) nests parasitized. In parasitized nests, 57% (8 of 14) of Brewer's Sparrow and 77% (49 of 64) of Sage Thrasher nestlings were afflicted. Early Sage Thrasher nests were more often parasitized by blow flies than later nests. The majority (87%) of parasitized Sage Thrasher nests were observed before the mean fledge date (9 June 1989, 10 June 1990). Shields and Crook (1987) reported an increase in parasitism of Barn Swallows (*Hirundo rustica*) through the nesting season, but Eastman et al. (1989) found no seasonal variation in parasitism of House Wrens (*Troglodytes aedon*). No seasonal patterns can be derived from the small sample of parasitized Brewer's Sparrow nests.

In this study, larvae were most often found on the wings (67% of 57 nestlings) and frequently at the base of developing primary feathers. Larvae were also found on the face (28%) and head (23%) as well as the body (19%), legs (12%), back (12%), neck (4%), and feet (4%) of nestlings. Individual nestlings frequently had *P. braueri* larvae at several locations. Larvae appeared to live on their hosts, i.e., they were visible, for at least four days.

The parasite load per individual nestling averaged 2.6 (SE = 1.2, range 1–6) for Sage Thrashers and 2.5 (SE = 1.4, range 1–7) for Brewer's Sparrows. Larvae were collected directly from nestlings of both host species. The larvae were often fully developed by the time young fledged, and larvae would frequently abandon their hosts while the birds were being handled. Collected larvae were preserved in alcohol or reared to adults.

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ORNITHOLOGICAL LITERATURE

PHYLOGENY AND CLASSIFICATION OF BIRDS: A STUDY IN MOLECULAR EVOLUTION. By Charles G. Sibley and Jon E. Alquist. Yale Univ. Press, New Haven, Connecticut. 1990: xxiii = 976 pp., 385 figs. $100.—The present and future of the science of phylogeny lies in molecular biology. Over the past 20 years, avian systematics has undergone a renaissance driven by the development of sophisticated technology that began with analyses of tissue and egg proteins and continues now with the newest technique—DNA hybridization.

DNA (deoxyribonucleic acid) is the molecular material which provides the blueprint for the synthesis of all protein and, therefore, is the genetic basis of most of the organisms on Earth. Each single strand of DNA consists of a series of nucleotides composed of three subunits—a sugar, a phosphate group, and a nitrogenous base. The sugar-phosphate groups comprise the backbone of each strand. Normal double-stranded DNA molecules consist of two single strands of DNA wound around each other in the familiar Watson-Crick double helix. In double-stranded DNA, each base of a nucleotide in a single strand is attached to a base in the other strand, forming a ladder-like structure in which the rungs are base pairs. There are four base species, but only certain bases will form base pairs. The base pairs contain the genetic code in groups of three (triplets) along single strands, and it is from this that the cellular machinery obtains templates for formation of protein. Complimentary single strands of DNA, therefore, bind to one another virtually perfectly. If double-stranded DNA is broken down to the single-strand form, it will reform spontaneously, and the single strands will be tightly held to one another as a result of the chemical bonds between the bases. DNA hybridization techniques are based on this principle.

In DNA hybridization studies, single-stranded DNA from two species are mixed and allowed to reform the double-stranded helix. Methods are then used that measure the strength with which the hybrid strands bind (melting temperature of the hybrid duplex molecule). Strands from similar species have many corresponding sections and bind strongly. Strands from dissimilar species bind weakly. The strength of binding is measured and used to construct appropriate phylogenies. This technique is especially important because it obtains measurements directly from the source of all genetic differences. This is, DNA-DNA comparisons provide insight into phylogeny because evolution produces changes in base sequences. There is reduction in the melting temperature of hybrid DNA molecules that is in proportion to the number of base sequence differences. The more differences (and lower temperature), the longer ago the two species shared common ancestry.

The present book is an unusual combination of elements. It is partly a textbook of molecular phylogeny and partly a report on one of the most exhaustive data sets I have seen. Sibley and Alquist devoted 11½ years to the continuous production of DNA-DNA hybrids in an effort to clarify the phylogeny of living birds. In the course of this work they produced 26,554 avian DNA hybrids representing approximately 2000 species of birds. The amount of work involved in obtaining and preparing samples alone appears staggering.

The authors begin the book with extensive sections on the history of DNA analysis, including the basic chemistry of genetic materials, structure of DNA, gene structure, and genetic regulation. They describe in detail DNA hybridization techniques, sequence of the genome, families of repeated DNA, comparative DNA studies and, finally, their materials, methods, and data analyses. They discuss their findings in light of molecular evolutionary "clocks," demographic factors, and the rate of DNA evolution. It is not until after 17 chapters (all of which are extremely rich sources of information on avian phylogeny and the analyses of DNA), that they arrive at the results of their extensive data set. The closing section is

one of the best, most understandable summaries of the importance of vicariance/dispersal that I have seen.

The book is exemplary in its thorough, detailed presentation of the results of these measurements. The authors present in 385 figures the graphic representation of their data sets and various cladistic diagrams of the relationships of different groups of birds. The huge number of figures is matched by the extensive reference section and comprehensive presentation of background materials for each taxonomic group. Historical background is presented in numerous instances and provides additional insight into the phylogeny and taxonomy of avian groups.

That this book is important goes without saying. However, it is also very well written and definitely is not boring. Non-avian biologists will benefit from its introductory sections. New students of avian phylogeny, evolution, and systematics should get their copies now. Older students will profit from it also; my ornithological lectures on the evolution and systematics of birds will benefit from my use of the book. The book offers little to the non-scientist, although some of the chapters may be useful to those with advanced interests in the relationships among major groups of birds.

The book is expensive, but it is long in quality and appears to be well worth the money. The typesetting and format are clear and pleasing. I detected no typographical errors, although there must be a few in such a long text. The book is nicely bound and has an attractive dust jacket. It should endure on the shelf very well, even though it will be used a great deal by many of us.

All-in-all, this is a monumental book which, in my opinion, qualifies as one of the major ornithological contributions of this generation.—Charles R. Blem.

African Birds of Prey. By Peter and Beverly Pickford (photos) and Warwick Tarboton (text). Cornell Univ. Press, Ithaca, New York. 1990:227 pp., 170 color photos with captions, 81 range maps, 81 drawings and silhouettes, $45.00 (cloth).—While not a "coffee table" type book, nor one heavy on bird biology, Pickford and Tarboton have nonetheless made a good compromise between the two and thus a fine gift book. The text does give a good lightweight flavor of raptor biology for the selected species and a blend of science and photographic art. This is not really a book on birds of prey of the continent of Africa, as the title might suggest, but rather of those raptors in southern Africa south of the Kunene, Okavango, and Zambezi rivers. So, of the some 92 diurnal raptors and 29 nocturnal raptors of Africa, 69 diurnal and 12 nocturnal species are covered. Three, the Cape Vulture (*Gyps coprotheres*), Black Harrier (*Circus maurus*), and Jackal Buzzard (*Buteo rufofuscus*) are given as endemic to the region. (Some authors include the Jackal Buzzard as a race of a wide ranging form that includes what Tarboton calls the Augur Buzzard [*Buteo augur*] in this text.)

The layout is visually pleasant. For the most part there is a page of text accompanied by either a single or, more frequently 2–3, photos of each species. An extensive appendix has a single column of text per species and provides a brief summary of the name, size, identification, habits, distribution, status, breeding, food habits, and voice, followed by a distribution map and a ventral drawing of the falconiformes in flight or a perched silhouette for the strigiformes. There is also a list of further readings and a glossary.

The book is a joint product of a team of photographers and the text by a professional biologist. As such, it requires two assessments; the photos and the text. By comparison with the quality of photos available of African species or those in similar recent books (Hollands, D., Eagles, hawks and falcons of Australia, T. Nelson, Victoria, 1984; Newton, I. [consulting

ed]., Birds of Prey, Facts on File, Inc., New York, 1990), the book is disappointing. The quality of the photos or what they depict of the species varies enormously. In some cases, the immature plumage is shown, in others the adult plumage. The photos of the Bearded Vulture (*Gypaetus barbatus*), Black Harrier, Lizard Buzzard (*Kaupifalco monogrammicus*), Cape Vulture, and Barred Owlet (*Glaucidium capense*) are, for example, excellent illustrative photos that either depict the bird well or the species in its habitat. On the other hand, the Gray Kestrel (*Falco ardosiaceus*) and Bat Hawk (*Maceiramphus alcinus*) are so shaded or dark that one can not get a flavor for those species. Because of the position of one frontal pose and hidden legs of the Booted Eagle (*Hieraaetus pennatus*), it is hard to distinguish it from the North American Red-tailed Hawk (*Buteo jamaicensis*). The flight photos are, for the most part, pleasantly in focus. Overall, the photographic contribution to the book is only average.

The text is very good within the limits of its purpose. Warwick Tarboton is an extremely knowledgeable biologist with extensive experience with raptors. He provides some valuable insight to each species. There seems to be no consistent format for the text, which is all right. Rather, those portions of the species biology that the author deemed important are given. The text seems to be relatively error free. I did find what may have been an editorial error in calling the Peregrine Falcon *Peregrinus falco minor* rather than *Falco peregrinus minor*. There is also some misinformation in the same species account by stating that an entire subspecies (*F. p. anatum*) became extinct in North America because of chemical poisoning. It is true that populations or portions of that subspecies were lost during that time period.

Overall, the book makes a contribution to one's library, and while a bit over-priced because of its drawbacks, it is not out of line with similar books and by today's standards.—Clayton M. White.

Owls of the Northern Hemisphere. By Karel H. Voous, illus. by Ad Cameron. William Collins, London; Massachusetts Institute of Technology, Cambridge. 1988:320 pp., 50 color plates and as many full page plates of sketches, usually several to the plate; 24 maps, 25 × 34 cm. $60.

Owls: Their Life and Behavior. By Julio de la Torre, illus. by Art Wolfe. Crown Publs., New York. 1990:ix + 214 pp., 175 color photos. 24 × 32 cm. $35. Foreword by Roger Tory Peterson.—The owls of the Northern Hemisphere have recently been the subject of a number of books. Seven of the species are common to North America and Eurasia, while some of the others, such as the Great Horned Owl (*Bubo virginianus*) and the Northern Eagle-Owl (*B. bubo*), are closely related. In the Old World, aside from the extended treatment of owls in vol. 4 of the "Birds of the Western Palearctic" and vol. 9 of the German "Handbuch," one has Mikkola's fine "Owls of Europe." In America, there is the inevitable volume by Paul Johnsgard; for a generally laudatory review of it see this journal, 1990:192–193. The overly promoted "Owls of North America" by A. W. Eckert and K. E. Karalus (artist) is hardly worth mentioning except to express sympathy for an artist asked by a naive author to provide full page plates for 18 subspecies, real or imaginary, of the Eastern Screech Owl (*Otus asio*) and 11 of the Great Horned! Turning to the two volumes at hand, Dr. Karel Voous, Holland's best known ornithologist, was asked in 1981 to provide a text for a portfolio of plates of owls of the Northern Hemisphere by a countryman. Ad Cameron. Not to be hurried (the book appeared in 1988), Voous, a longtime student of the Strigidae, has written a lengthy, authoritative, and in some ways, pioneering book. Taxonomy, distribution, zoogeography, ecological interactions, and the physiology and anatomy of hearing and vision all

receive in-depth treatment. Nor are other aspects of natural history neglected. The account of the Tawny Owl, for example, runs to an estimated 6200 words. Species such as the Stygian owl (*Asio stygius*), the African Marsh Owl (*A. capensis*) and the Brown Fish Owl (*Ketupa zeylonensis*), which have only a talon hold in the Northern Hemisphere, have been included—47 species in all—so one has a sampling at least, of almost all the genera of the family.

Mr. Cameron's paintings I would call good, but not inspired. Of equal or perhaps greater interest are his sketches and drawings, usually several to the plate, of various activities and postures. One, for example, shows four incubating owls of as many species, one a Great Gray Owl (*S. nebulosa*) on an old Northern Goshawk (*Accipiter gentilis*) nest, the other three ground nesters, including an eagle owl, while a smaller owl surveys them warily from the entrance of its nest cavity. It is unfortunate that this is such a big, massive, expensive book. To be sure, the MIT Press (yes, they actually published a book on owls) quickly became nervous and remaindered the $60 volume at one-third price before it had a reasonable run for the money.

In the second book here under review, the tail also wagged the dog in that the author was engaged to provide a text for illustrations—this time color photographs by Mr. Art Wolfe, who, the jacket tells us, is "the world's foremost photographer of owls"! He has hitherto hid his candle under a bushel, but one readily admits that all of his photos are technically excellent. Perhaps we have too many owlets lined up on limbs (of their own volition?) but there are excellent takes of adults also. I half expected to find a few scarce or local species such as the Whiskered Owl (*O. trichopsis*) or the Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) omitted or glossed over, but, no, they are all here. Someone was very good at finding nests! As to the jacket claim, several photographers have taken unsurpassable shots of owls.

Anyone who knows Julio de la Torre would expect the text to be racy, even slangy, and that it is. But Julio is a genuine longtime owl enthusiast and he has done his homework as well. Recent changes such as the relentless advance of the Barred Owl (*Strix varia*) to the Pacific are discussed. He provides some extras, such as a chapter on fossil owls in which the giant owl of the Cuban Pleistocene, de la Torre's former homeland, needless to say, gets attention. Nor is the author adverse to speculations—such as the interesting one that the Northern Hawk-Owl (*Surnia ulula*) is an oversized relative of the pygmy owls. While one might ask for confirmation of a few statements, "Owls, Their Life and Behavior" provides a colorful, popular introduction to these birds.—D. Amadon.

Food Hoarding in Animals. By Stephen B. Vander Wall, illus. by Marilyn Hoff Stewart. University of Chicago Press, Chicago, Illinois. 1990:xii + 445 pp., 166 numbered text figs., 24 tables, 2 appendices. ISBN 0-226-84735-7. $76 cloth, $29.95 paper.—This highly commendable book is the first taxonomically comprehensive, and the most exhaustive, synthesis of the vast and scattered literature on evolutionary, ecological, and behavioral aspects of food storage in animals. Food hoarding, which Vander Wall defines as the handling of food in ways that conserve it for future use, is a key component of the integrated adaptive strategy of many birds, mammals, and arthropods. Vander Wall reviews the current state of knowledge on a wide variety of topics, such as the reproductive benefits accruing from the use of stored food, the ultimate causation of food hoarding, the cache-protecting behaviors used by food-hoarding animals, the internal and environmental influences on hoarding behavior, the role of memory in the retrieval of scattered food stores, the effect the storage of plant propagules has on the dispersal and establishment of plants, and the impact food hoarding may have on community structure. In addition, he devotes three chapters to an overview

of the hoarding behavior and related natural history of animals within three taxonomic groups—birds, mammals, and arthropods. Ornithologists will be particularly interested in Chapter 9 ("Food-hoarding Birds"). In that chapter, Vander Wall reviews the literature documenting the food hoarding behavior of 100 bird species from 15 families, particularly the Corvidae, Paridae, Falconidae, Strigidae, Laniidae, Sittidae, and Picidae.

Aside from being the most recent and most thorough review of hoarding behavior, Vander Wall's well-written book differs from several excellent earlier reviews in two ways. First, in addition to summarizing what is known about food storage in vertebrates, "Food hoarding in animals" brings together what is known about mass provisioning in spiders, ants, bees, wasps, and beetles. Second, in addition to summarizing the literature on the ecological and evolutionary aspects of hoarding, the book provides an overview of the psychological literature concerning the proximate control of food hoarding. The psychological literature has been largely ignored by behavioral ecologists working on food-hoarding problems. Vander Wall calls for comparative studies on the regulatory mechanisms of hoarding across species. Since publication of his book, two excellent studies have used dynamic programming models to explore how internal states of the animal and environmental factors may influence daily rhythms in the storage and retrieval of caches as well as in body mass (McNamara et al., Behav. Ecol. 1:12–23, 1990; Lucas and Walters, Anim. Behav., in press). This approach to the study of dynamic aspects of hoarding behavior as controlled by internal states and environmental conditions seems to hold great promise.

For behavioral ecologists actively working on food-hoarding problems or planning to do so, Vander Wall's book is nothing short of a treasure, and it deserves a very enthusiastic recommendation. Part of the book's value is that it is an abundant source of ideas for future research. The bibliography of nearly 1500 cited works, as the publisher claims, "is itself an invaluable and unique reference." The books readership, though, should extend well beyond behavioral ecologists who have a specific interest in food-hoarding behavior. Certainly, anyone with a broad interest in behavioral ecology or ornithology should find much of value.—Thomas A. Waite.

Guide to the Birds of Madagascar. By O. Langrand. Yale Univ. Press, New Haven, Connecticut. 1990: 364 pp., 40 color plates, 6 line drawings, 4 figures, 3 tables, 205 maps, $50.00.—The island continent of Madagascar has long been of interest to field biologists. The flora and fauna of this mysterious island is highly distinctive, indeed almost bizarre. The real possibility that human pressure on the land may cause the extinction of a considerable portion of this biota in the near future fuels our interest and concern. Despite this interest, little has been published in English on the birds of Madagascar since A. L. Rand's magnificent summary of the 1929–1931 Mission Zoologique Franco-Anglo-Américaine Madagascar Expedition (1936, Bull. Amer. Mus. Nat. Hist. 72:143–499). The only other recent comprehensive treatment of the Malagasy avifauna, volume 35 of the *Faune de Madagascar* series (P. Milon, J.-J. Petter, and G. Randrianasolo, 1973), is written in French and is difficult to find; this has left a considerable void in the literature on Madagascar, which Langrand's book readily fills.

Olivier Langrand is uniquely qualified to write such a field guide. Since 1980, he has travelled extensively throughout the island. He has authored or co-authored an important series of papers on the conservation status of some of Madagascar's rarer birds—the plight of the highly endangered Madagascar Fish-Eagle (*Haliaeetus vocifroides*) was first made known through these studies, for example—and it is only fitting that the sum of Langrand's extensive knowledge of the avifauna be brought together in one volume.

This guide begins with a useful overview of the vegetative communities of Madagascar and their distribution; this is followed by a discussion of the distribution of birds in relation to these communities. Biologists who have not visited Madagascar may not be aware that Madagascar does maintain, with varying degrees of effectiveness, a system of natural reserves and parks; these protected areas are briefly described by Langrand. The introduction concludes with a brief guide to 17 bird-finding sites in Madagascar, which is supplemented by a table listing the species recorded at these sites.

The major part of the book is taken up with accounts, geared towards field identification, of 256 species recorded from Madagascar; 24 additional seabirds or waterbirds that might occur in Madagascar are discussed briefly as well. Latin, English, French, and Malagasy names are provided for each species. The accounts include the following sub-headings: description; identification; behavior; voice; habitat; diet; nesting; and distribution and status. For 200 species (the bulk of the regularly occurring avifauna), the distribution information is supplemented by a small map of the species' range; these maps are gathered together in a separate section near the end of the book. These accounts contain a considerable amount of valuable information on the natural history of each species. I would be curious to know how much of this information is original and how much has been gleaned from the literature; unfortunately, as this part of the book adheres to standard field guide format, references are not included in the text. The book reads well; thanks are due to Willem Daniels, for translating the text from the French, and to the Smithsonian Institution for subsidizing this translation.

The 40 color plates by Vincent Bretagnolle illustrate the regularly occurring species. These plates vary in quality, and although all are adequate for the purposes of identification, some fail to get across the "essence" of the birds portrayed. In some cases, in fact, such as the Madagascar Wood Rail (*Canirallus kioloides*) shown resting on its haunches, the illustration might give a misleading impression of the birds' comportment. The plates are not all drawn to the same scale, which is acceptable, but given that, it would be useful to have some kind of scale bar on each plate. It can be disconcerting to see the jeries (Plate 36) reproduced so that they appear to dwarf the greenbuls (Plate 32), although in life the greenbuls are several times the size of a jery. Although all species on any one plate are said to be to the same scale, this policy does not appear to be held to in all cases (especially on Plate 35). Among the rarer species that are portrayed in the plates are the Snail-eating Coua (*Coua delalandei*), which has not been observed in 150 years, and such scarcely better-known species as Madagascar Serpent-Eagle (*Eutriurchis astur*), Madagascar Red Owl (*Tyto soumagnei*), and Red-tailed Newtonia (*Newtonia fanovanae*). At the time that the book was written, this newtonia was known only from the unique holotype, but it has recently been re-discovered at two widely separated sites. As field biologists have good reason to be on the lookout for this species, it is unfortunate that the depiction of the Red-tailed Newtonia fails to capture the birds' remarkable resemblance to the female Red-tailed Vanga (*Calicalicus madagascariensis*).

Given Langrand's residency in Madagascar, the logistical problems of bringing this book to press must have been considerable. Greater attention to detail on the part of the press would have caught some of the almost inevitable errors or omissions. The distribution map for the Collared Nightjar (*Caprimulgus enarratus*), widespread (but scarce) in forests of eastern Madagascar, is completely blank. The columns in Fig. 3 are not identified. Also not explicitly identified are the line drawings that illustrate a handful of species that are vagrants to Madagascar. In most cases, this is not a problem—there is only one species of oriole recorded on the island, for example—but I am guessing that the unidentified swifts on page 232 are Mascarene Swiftlets. (*Colluralia francica*) The distribution maps are identified not by the name of the species, but by the sequential number that each species is assigned in the text. Consequently the maps can not be identified without constantly flipping back and forth in the book, which quickly becomes burdensome.

The classification of the Malagasy avifauna, especially of the passerines, is to a considerable degree unresolved. Langrand wisely avoids making many new arrangements in the sequence of species, but I was surprised to see the jeries (*Neomixis, Hartertula*) in the Sylviidae rather than with the babblers (Timalliidae). While this arrangement may be no more right—or wrong—than any other classification in use, I am not aware of a recent precedent for this sequence.

A nice feature of the book is an etymology of many of the Malagasy bird names; a majority of these are onomatopoeic.

I highly recommend this book to anyone who visits Madagascar. Langrand is to be congratulated on a job well-done. This book represents one of the most important steps for spurring international interest in the biology and conservation of the poorly known, fascinating, and threatened avifauna of Madagascar.—Thomas S. Schulenberg.

Natural History and Management of the San Clemente Loggerhead Shrike. By Thomas A. Scott and Michael L. Morrison. Proceedings of the Western Foundation of Vertebrate Zoology, Volume 4, No. 2, Western Foundation of Vertebrate Zoology, Los Angeles, California. 1990:35 pp., frontispiece, abstract, 10 tables, 10 figures (5 photographs), 3 appendices. $ 5.00.—Loggerhead Shrike populations have decreased across much of North America, thereby providing the stimulus for research on several declining populations. This monograph makes a significant contribution to our knowledge of one of these populations, the San Clemente Loggerhead Shrike (*Lanius ludovicianus mearnsi*), an endangered subspecies endemic to San Clemente Island, California.

Professionals, particularly those interested in endangered species and studies of insular birds, will benefit greatly from this publication. Recreational ornithologists, however, may lose interest when working through the numerous tables, figures, and statistics.

This publication stemmed from a five-year study which investigated the natural history and population ecology of the San Clemente Loggerhead Shrike, so as to allow for comparisons with stable populations of mainland shrikes. The objectives were to identify factors that may have precipitated the decline of this subspecies and to develop management recommendations for preservation of the endangered birds. Five major areas of study are listed as subheadings in the "Results and Discussion" section. They include shrike occurrence and abundance, population biology, foraging behavior, breeding behavior and nest predation, and nesting habitat and the effect of browsing animals.

The authors provided excellent information on the current status of the population and a concise quantitative description of the environment which the San Clemente Loggerhead Shrike inhabits. By examining the behavior of shrikes, as well as the environmental factors affecting them, the authors were able to identify constraints that likely preclude population growth. Based on this solid quantitative foundation, the authors developed a detailed management strategy that could be implemented to reduce population constraints. As with some other island systems, exotic animals appeared to play a significant role in the degradation of native flora and fauna. The authors suggested that habitat could be improved by removing goats and by direct supplementation of shrubs. They outlined specific guidelines for the propagation, establishment, and maintenance of shrubs so as to maximize their effectiveness. The authors also suggested that shrike reproductive output be enhanced through double-clutching and the release of captive-reared young. Finally, they proposed that the survival of shrikes be increased through direct predator removal. Although attempts at removing predators in other areas have often proved impractical, the authors outlined a specific approach designed to be feasible on San Clemente Island.

Criticisms of this work are few; however, it should be noted that an explicitly stated assumption of this study was that differences between the declining population of San Clemente shrikes and those of stable mainland populations would allow for the identification of factors contributing to the San Clemente shrikes' decline. Although this comparative method represents a valid approach, it is unfortunate that the authors frequently included comparisons between the declining San Clemente Loggerhead Shrike and several mainland shrike populations which are not stable, but are also reported to be in decline. This does not reduce the validity of the authors' study, however, it does leave conclusions about the significance of these comparisons up to the reader.

In summary, this timely, well-written document makes a significant contribution to our knowledge of the San Clemente Shrike. Numerous subheadings, appendices, and concise tables and figures make it easy for the reader to extract specific information. Also, photographs of the habitat provide a good qualitative sensc of what the area is like. The wide range of topics covered in this paper relative to other scientific literature on shrikes makes it a contemporary complement to the 1931 monograph by A. H. Miller.—Dale E. Gawlik.

The Manx Shearwater. By Michael Brooke. Illus. by Dafila Scott. T. & A. D. Poyser, London. U.S. edition. Academic Press Inc., San Diego, California. 1990:246 + xviii pp., 39 numbered black-and-white figs., 56 tables. $32.50.—My first encounter with a Manx Shearwater (*Puffinus puffinus*) was on a quiet summer night in the Faeroe Islands. I was listening to the soothing purrs and trills of the storm-petrels, when something shot past my ear and thumped onto the ground, screaming like a bat-out-of-hell with whooping-cough. I nearly fell off the cliff.

This is how Michael Brooke meets them all the time, and he has the scars to prove it. Brooke is a senior Oxford University zoologist, at the Edward Grey Institute of Field Ornithology, who has spent half his lifetime studying this intriguing seabird. Most of his work has been done on Skomer Island in the Irish Sea, off the south-west tip of Wales. But shearwater research there, and on Skolkholm nearby, goes back fully 60 years, to Ronald Lockley's classic studies in the 1930s. There have been breaks in continuity, notably during World War II, but the Manx Shearwater remains one of the best-studied birds.

Brookc summarizes the astonishing breadth of this research. He begins with the distribution, taxonomy and morphometrics of the Manx, with reference to its related subspecies and species. His data go back far enough for him to test for the inheritance of body characteristics, and there is evidence for this in tarsus size. However, his principal interest is in the birds' breeding ecology and population ecology. Most of his chapters are given over to aspects of this: from the pairs' burrow choice in March, and the females' pre-laying exodus, until parents and chicks abandon Skomer in September. Incubation and fledging success, the efficiency of experienced and inexperienced parents, chick growth rates, and artificial twinning experiments are some of the topics that he tackles along the way.

On the behavioral side, Brooke describes the birds' calls, in lyrical terms that I wouldn't use myself, and speculates about their functions. He also describes his experiments on the range of the birds' senses, testing how they find their burrows in the dark. (Mainly by sight, it seems; smell plays little or no part.) And he summarizes Geoffrey Matthews' classic homing and navigation experiments in the early 1950s, using Manx Shearwaters taken from burrows on Skokholm and released as far away as Boston (p. 7). One of the Boston birds came home, 3200 miles, in only 12.5 days—a feat of directed navigation if ever there was one. On a different tack, Chapter 8 discusses puffinosis, a chronic affliction of Manx chicks whose epidemiology has proved singularly hard to unravel. Brooke also summarizes the history

of the birds' exploitation by man. Young Manx Shearwaters, fat and almost ready to fly, were a combination of food, fertilizer and lobster-bait for the Norse-Celts of the Middle Ages, clinging to their arc of barren islands from the Scillies to Iceland. The harvest ended long ago, but in its time, it was the ruin of the giant colony on the Calf of Man in the Irish Sea. This, probably the biggest colony ever, was where the abundance of Manx Shearwaters gave the species its English name—and once scared hell out of a Viking war-fleet. The old harvest has an odd, modern successor on Rhum, in the Hebrides, where red deer (*Cervus elaphus*) come down from the hills at fledging time to catch chicks sitting outside their burrows (p. 49). Rhum has poor grazing, but the birds' bones are rich in the minerals that the deer need.

Don't be put off by the book's Introduction: a good idea which doesn't quite work. Here, Brooke tries to summarize all these disparate topics for you in advance, and the result is predictably jerky. However, the specialist chapters that follow read smoothly enough. I question the odd point of detail, of course. For instance, I don't agree with Brooke's paradox (p. 29) that it's the least aerially adapted shearwaters, like Manx, that make the longest, transequatorial migrations. Cory's Shearwater (*Calonectris diomedea*), which we both agree is the most aerial shearwater in the North Atlantic, crosses the Equator to Argentina in January. I'm no economic historian, but (p. 42) I don't think Brooke can estimate the harvest of Manx chicks on Skokholm in 1387–1388, by dividing the revenue they yielded by the price per bird in 1660—and on the Calf of Man at that! I'd like to see some direct information on the birds' pelagic ecology, along the lines of our work with Greater Shearwaters (*Puffinus gravis*) off Nova Scotia, as opposed to deductions based on long-distance movements (Chapter 4) and food deliveries to the colony (Chapter 7). But, as far as I know, the information simply isn't there yet. However, these are quibbles. Overall, I found 'The Manx Shearwater' clearly written and full of an unexpected variety of interesting information. I wish Michael Brooke every luck with his bands, his flashlight, and his little fluorescent socks, and I recommend his book to all field ornithologists, marine and terrestrial alike.—Richard G. B. Brown.

Birds in Art: The Masters. By Inga Brynildson and Woody Hagge. Leigh Yawkey Woodson Art Museum, Wausau, Wisconsin. 1990: 127 pp. $24.95.—This book commemorates the Leigh Yawkey Woodson Art Museum's fifteen years of providing the *Birds in Art* exhibition. Selected bird art by international artists has been exhibited annually since 1976. In addition to the commemoration, the book honors 14 Master Artists selected by the Museum (one annually). I agree that those selected are indeed "Master Artists."

The volume is 12¼ × 9¾ in. (17.2 × 13.7 cm) with the spine on the short side. The covers are white binders cloth; a blue stamp of the Northern Mockingbird (*Mimus polyglottos*) logo of the Masters Medal is on the upper front cover; the end sheets are soft blue; "Birds in Art The Masters" is stamped on the spine, along with a small box, lettered Leigh Yawkey Woodson Art Museum. The shiny blue paper dust jacket repeats the Masters Medal logo in silver on the face, and lettering from the spine on the dust jacket spine. The back of the dust jacket lists the 14 honored Master Artists, repeats the box from the spine, and shows the ISBN number. A text of 127 pages, 85 color plates, 4 pages of references including publication notes and acknowledgements complete the offering.

The layout of the text is excellent. Set up in two parts, the first covers only ten pages and includes the Foreword in which Kathy Kelsey Foley, the Museum Director, deftly puts the book in perspective, particularly giving credit to all who made the celebration possible. The Preface is concerned with the "coming of age" of wildlife art in America and the role that the Museum has played and continues to play. Birds in Art—Taking Flight deals with the

genesis and growth of the "Birds in Art" concept. The Flight of the Painted Bird is a historical assessment of bird art from cave paintings in Spain to limited edition prints of today available at the local frame shop.

The title page indicates Inga Brynildson and Woody Hagge as the authors but they were, in fact, primarily editors since only six pages of text are their words exclusively. However, those pages are informative, well documented, and written in a very pleasing style. Editing the commentary provided by the Master Artists was no mean undertaking for Inga and Woody, particularly to accommodate the format of the book with the various written contributions of the artists.

The major portion of the book (112 pages) is entitled *The Masters.* Fourteen artists contribute enlightening personal reflections on painting, fine art, illustration, conservation, science, art appreciation, etc. Each artist's comments are presented on two tri-column pages, and each text is followed by six full-page reproductions of his artwork, including photographs of sculpture by the two artists working in three-dimension. The unnumbered plates are identified by title, species, medium and surface, ownership, and date the paintings were shown at a *Birds in Art* exhibition. Below each painting is an appropriate quotation from the preceding text; a very fine editorial touch.

There was great temptation for me to deal with the paintings, but my comments will concern only the artists' narratives. Each artist's text is headed by his photograph, date and place of birth, and residence or date of demise.

The first Master Artist was Wisconsin's own fiesty artist-conservationist, Owen J. Gromme. He says, "I try to demonstrate in paint what Aldo Leopold so beautifully demonstrated in words." Who can deny that he has achieved a large measure of success? He also states quite naturally, "I paint because I love it. It's as simple as that." Other Masters have echoed those sentiments.

I was shocked by the singularly unflattering photo of my friend, George M. Sutton, who was always smiling with a bright and pleasant countenance. This consummate gentleman artist was a serious student of ornithology. He claims, "I've never been able to disassociate painting from bird study." Inspiration aside, Sutton says, "The very force which drives me, at times relentlessly, to do the best I can at drawing birds is Fuertes." Louis Agassiz Fuertes, America's premier wildlife painter, was Sutton's mentor. There could have been none better for any bird artist.

Roger Tory Peterson is a household name among ornithologists, bird watchers, and bird artists. Known internationally for his bird identification handbooks, he records quite candidly, "I feel a greater sense of friendliness, ease, and camaraderie when I am in the company of wildlife artists than I feel with any other group—and that includes the hotshot birders and professional ornithologists."

Don R. Eckelberry with a keen philosophical outlook advises: "To young painters, I would say look at everything as though you have never seen it before." Of the visual appearance of a painting he points out: "It is not what is seen but *what is felt* in what is seen that counts; in other words, not sight but insight." Thus the eye must guide the heart.

Sir Peter Scott, who has no peer in the painting of waterfowl and their habitats, was a foremost global conservationist. His wish: "I hope the viewer derives as much pleasure out of seeing my art as I, as an artist, have derived out of seeing my subjects." To view a splendid Scott canvas is eminently pleasurable as both art and ornithology.

Arthur Singer was inspired by many fine wildlife artists, including Louis A. Fuertes and Carl Rungius. He stated what some artists may wish to avoid, namely that "Selling prints is a business and sometimes you compromise to paint what the public wants." Critics of wildlife art feed on such an attitude long recognized but rarely admitted.

Robert Bateman is not only a superb artist but an articulate writer who uses the metaphor

as skillfully as he does a liner brush. Of his mental preparation he claims, "I try (when painting chickadees mobbing an owl) to get into the skin of the chickadees." He has been in a good many skins, and we art viewers are the better for it. (I wonder if most artists believe that an art critic to review accurately tries to get into the skin of an artist[s]. I know he often gets "under their skin.")

Guy Coheleach confirms a long held conviction of mine, that drawing is the prime basis for graphic art, when he cautions, "The biggest mistake beginners make is not learning to draw." A fun loving free spirit, he enjoys the field aspect of painting, but says ". . . I dread the time I must spend in the studio."

Charles Greenough Chase regards his art thus: "I call what I do pure sculpture or subtractive sculpture." What follows in his text is a folksy discussion of technique in an effort to differentiate between wood carving and wood sculpture. He ends his piece with the most humorous anecdote in the book.

J. Fenwick Lansdowne's assessment of his artistic skills is forthright and precise when he says, "I do bird portraits. I do fairly tightly controlled pictures with a lot of detail, a lot of exactitude." If, therefore, one were to conclude that his paintings are less exciting than loose impressionism, one would be in gross error: Fenwick Lansdowne is an excellent painter.

Keith Shackelton is an outstanding painter of seascapes. The fascination for such painting, he concedes is ". . . because they [the seas] satisfy the frustrated abstract painter that lurks within most realistic painters." Shackelton's realistic bird paintings, however, are far from ordinary. He has mastered the technique of using blue and white oilpaint to create a fascinating world of ice, snow, sky, and water.

The driving force behind Kent Ullberg's sculptures is the overwhelming desire to communicate his artistic feeling. This painter's son became a sculptor when ". . . I got my hands in clay, I fell in love instantly—really never looked back." The magnificent bronze eagle on the front lawn that welcomes one and all to the Leigh Yawkey Woodson Art Museum in Wausau is an Ullberg creation.

Lars Jonsson is the youngest Master Artist, but his statements on art are sage indeed. "Wildlife art that does not reveal something about the artist is very seldom significant." Of the artist he writes, ". . . art is the life you give to each painting." If ever there be an artist to equal the eminent Bruno Liljefors, it will most likely be Lars Jonsson.

Maynard Reece has won the Federal Duck Stamp competition an unprecedented five times, underlining his skill in waterfowl portraiture. Artists Francis Lee Jaques and Jay "Ding" Darling were the primary guiding forces for Reece, who had no formal art training. His statement, "Good illustration should be good art" is a worthy observation.

Some of the Master Artists indicated that they had no formal art training. They all express a love for their work, consider outdoor activity essential, were influenced by other artists, had an early proclivity for art, and would prefer to be called artists as opposed to bird artists.

This is a volume that provides the reader with insightful information about and by fourteen of the world's outstanding artists who specialize in bird painting. Their paintings in this volume subtly illustrate their commentary. All in all, this book is a bargain in artistic culture. Highly recommended!—Robert A. McCabe.

Seabirds of Hawaii: Natural History and Conservation. By Craig S. Harrison. Cornell Univ. Press, Ithaca, New York, 1990. 245 pp., 41 plates. $15.95 paper, $36.50 cloth.—*Seabirds of Hawaii* summarizes the available information on the breeding biology, feeding ecology, historical population trends, and conservation efforts for the assemblage of seabirds that nest within the Hawaiian archipelago. The Hawaiian islands are home to some 23 species of seabirds that together number several millions. There are few other islands in

tropical or subtropical waters of the North Pacific where these species can nest. Thus, the Hawaiian Islands are exceedingly important to the marine avifauna of the North Pacific Ocean. Sadly, several species are threatened or endangered.

In its first chapter, the author sets the scene with a discussion of the geological origin, oceanographic setting, and history of human occupation. In the second chapter, Harrison presents information on general aspects of seabird biology, including evolutionary history, population dynamics, and breeding and feeding ecology. In chapter three, he discusses the breeding ecology and the way it relates to specific conservation problems for each of the Hawaiian seabird species within the context of each family: albatrosses, petrels, storm-petrels, frigatebirds, boobies, tropicbirds, and terns. Finally, Harrison discusses conservation problems by detailing the laws established to protect birds, including seabirds, and the record that public agencies and officials have compiled in support of those laws.

There appears to be a statement, first, of Harrison's captivation by the allure of seabirds: the ecological rules of survival for these beautiful creatures in an environment inhospitable to most air-breathing animals and the pivotal importance of remote islands to success under those natural rules; and, second, of his frustration that government agencies and most officials are more aware of their vested interests than in fulfilling the duties of their office, namely, exercising authority under public laws of wildlife protection.

The first three chapters appear to be an attempt to convince the reader (wildlife officials and public servants?) that seabirds are worth protecting. In this portion of the book, the reader must be very knowledgeable about marine ornithology to know the source of the material and statements, because the material is not documented or referenced. It is accurate, however. The last chapter is an attempt to show that seabirds can be protected by other than passive means, i.e., by enforcement of existing laws and the appointment of persons knowledgeable about wildlife in wildlife positions rather than merely by passive means, i.e., the purchase of real estate on which seabirds may or may not nest. The last chapter is the only one in which facts are documented. Harrison details the actual statutes and law cases that bear on seabird conservation problems. Because of this emphasis, the book appears to be written primarily for the benefit of state and federal officials who are charged with protecting the populations and habitats of Hawaiian seabirds, of the conservation organizations that are just beginning to gain a foothold in Hawaii, and of Hawaiians who perhaps have yet to appreciate the natural treasures of their home and the limits needed to exploitation if these treasures are to last. That is not to say that those travelers to Hawaii interested in natural history won't find much of benefit in this book. It is clearly written, readable, well-edited, accurate, and illustrated with fine drawings and color photos.—David G. Ainley.

Birds of the West Indies (Oiseaux des Petites Antilles). By Édouard Benito-Espinal. Les Éditions du Latanier, Anse des Lézards, 97133, Saint-Barthélemy, F.W.I. 1990:128 pp., maps, 84 color photographs, graphs, line drawings. 100 French Francs.—This attractively produced little book has a field guide format that will fit easily even in small pockets (4.5 × 8.5 in.). Its hard cover is well bound and coated with a relatively waterproof plastic material. The text is bilingual, French and English, and very concise, containing adequate information about the region and brief descriptions of 84 species, migrant as well as resident, known to occur in the area.

The book contains a summary, foreword, preface, introduction, a general map of the Lesser Antilles, more detailed maps of Guadeloupe and Martinique, the topography of a bird, a short section on "What is a bird," the species section which forms the main part of the book, indices of scientific, French, English, and local names, and a short bibliography.

Each species is treated on a single page. One or several color photographs, usually taken by the author, illustrate each species. They are, in general, of good quality and represent the species well. French, English, Latin, and local names follow immediately after a short section outlining the characteristics of the family. This part is given only for the first species of a family. The text is sketchy but contains adequate information about identification characters and sometimes a few details about the ecology or the behavior of the species. The author provides for each species a map of the Lesser Antilles showing on which island(s) it occurs. In spite of their small scale, I find these maps very useful because all the islands are clearly identified and the range shows clearly. A graph listing nine of the islands and nine of the main habitats indicates where a species is to be found on a given island. In this part, the author does not distinguish between permanent resident and migratory or winter resident species, although the status of the species has been given in the text.

Overall this is a very good introduction to the birds of the Lesser Antilles, and the author must be congratulated for having done such a good job. The publisher equally deserves praise for the production of a book of this quality. I highly recommend this work to anyone interested in the fascinating birds of this part of the West Indies.—Henri Ouellet.

Nepal's Forest Birds: Their Status and Conservation. By Carol Inskipp. ICBP Monograph No. 4, International Council for Bird Preservation, 32 Cambridge Road, Griton, Cambridge CB3 0PJ, U.K. 1989:187 pp., 12 black-and-white bird illustrations, 9 figures, 14 tables, appendix. £8.50.—Although this treatise deals exclusively with forest birds in Nepal, mention is made of some species that have adapted to habitats modified by people. One of them, the Spiny Babbler (*Turdoides nipalensis*), perhaps the most famous bird in this Himalayan Kingdom, is characterized as being fairly common in dense shrublands throughout the country. But strictly forest birds have not fared so well because this once extensively forested principality decreased to only 43% forested land by the end of the 1970s. This figure would seem much too high to a traveler around Nepal, but is put into perspective with the author's definition of forest to include areas of scattered trees and shrubland, which is what much of the still remaining forests in Nepal seem to be. This concept certainly misses the requirements of birds dependent on large tracts of mature forest, a well-studied phenomenon in the New World.

In Nepal as in many places, the retreat of forests resulted from increasing human population pressure exerting basic needs for fuel energy, fodder and bedding for livestock (the trees are climbed and the foliage is regularly lopped for these purposes, like hay is mowed), and for construction. Consequently, it is surprising and encouraging to learn that around 10% of Nepal is under an extensive protected area system. The discouraging outcome of this is the realization that not all these preserves are well-protected against human intrusions and exploitations.

Against this backdrop, author Inskipp has done an absolutely superb job in presenting the details of forest stand structure and diversity in Nepal juxtaposed against corresponding avifaunal dependence, distribution, and current status. The various forest types are described in detail, the bird species occupying each type are enumerated, and the status of each bird as to whether at risk or not is indicated. From this we learn, for example, that out of the 850 species of birds in Nepal, some 469 are forest nesters and that Nepal holds internationally significant populations for nearly 120 of these. Unfortunately, 131 species are at risk, and 84% of these are forest birds, a testimony to the rapid rate of clearing forested lands. Thus 20 birds have become extinct in Nepal, and one formerly extensive subtropical forest type is nearly gone.

Besides admirably identifying conservation issues, this book in invaluable in another important way. It describes all the parks and wildlife reserves in Nepal and gives the bird list for each. It will beeome a valued referenee for birding tourists who flock to Nepal's parks.—Douglas A. James.

Rapaci in Volo, Liguria: Archeologia Probabile. (Birds of Prey in Flight.) By Luisella Carretta, Pirella, Genova. 1988:73 pp.—At one time or another, those of us who study birds have wished that we eould fly. Luisella Caretta shares this fantasy and relates her feelings and studies of five speeies of Italian raptors through text and watereolor. Beeause we eannot fly, we must fly vieariously through the birds we observe, study, and love. "Rapaei in Volo" is definitely a work of love by a sensitive and eareful observer. Reading this book brings Leonardo to mind; how he must have pondered birds and their flight.

Written in Italian with a parallel English translation, this book details the soaring behavior of five speeies of diurnal raptors that inhabit the Ligurian Apennines. For eaeh speeies, a short narrative is presented, with brief seetions on general natural history, hunting, and flight. Beeause it was written for a popular audienee, the seientific merit of the text is limited. A eolor "portrait" accompanies eaeh speeies narrative. Dozens of diagrams of flight paths of individual birds are ineluded, whieh may be considered ethograms. These diagrams also detail the topography, elouds, updrafts, and wind at the time of observation. Unfortunately, the watereolors and sketehes laek the detail most readers expeet from the field guides now available. I particularly liked the ehapter about flight and meteorology despite its brevity and some inaeeuraeies. Together, the drawings and text give the reader an appreeiation of how these birds fly.

This book was produeed in a large (24 × 33½ em; 9½ × 13 inehes), softeover format. The high quality paper makes the sketches and text erisp and clean, although the eardstoek from whieh the eover was printed will deteriorate with use. Overall, *Rapaci in Volo* should be a fun book for readers who have not observed raptors or other soaring birds.—Paul Kerlinger.

Briefly Noted

A Comunicação Sonora Do Anu Branco—Avaliações Eeo-etológieas e Evolutivas. By Hernán Fandiño Mariño. Editora da UNICAMP, Campinas, São Paulo, 1989:302 pp., 26 sonagram plates, 20 maps. Text in Portuguese. Priee not given.—This master's thesis by a Colombian resident of Brazil provides detailed deseriptions of the vocal repertory of both eaged and wild Guira Cuekoos (*Guira guira*) in Londrina, Paraná, and vieinity. Relation of the vocalizations to behavior is analyzed in considerable detail, with frequent referenee to works on avian eommunieation by E. Morton, D. Davis, W. Smith, S. Smith, and others. It is of particular interest that the São Paulo State University at Campinas is now publishing ornithologieal works in this attractive book format.—William Belton.

Birds of Prey in Virginia. A History of Specimen Records from 1853 to 1988. By David W. Johnston and William J. Ehmann. Virginia Avifauna No. 4, Virginia Soeiety of Ornithology, Lynchburg. (Available from VSO Publieations, % YuLee Larner, 1020 West Beverley St., Staunton, Virginia 24401.) 1990:58 pp. $9.00.—The authors inventoried specimens and other records of 24 species of birds of prey, ineluding the owls. Data are given for more than 1500 specimens including about 600 egg sets. In addition, there are 400+ records of

dead birds that were probably not saved. Analysis of these data revealed historically important changes in distribution and breeding sites. Interestingly, in light of the general decline of collecting about 477 of the records were made since 1960.—George A. Hall.

Changes in Breeding Bird Populations. Between 1930 and 1985 in the Quaker Run Valley of Allegany State Park, New York. By Timothy H. Baird. Bulletin No. 477, New York State Museum, Albany. 1990:v + 41 pp., 8 black-and-white photos and maps. No price given.—In 1930 and 1931 A. A. Saunders carried out one of the earliest breeding bird population studies as he surveyed the breeding birds of a large forested area in western New York. Timothy Baird has repeated Saunders' studies in 1983, 1984, and 1985 using methods identical with those of Saunders. During the 50 years the density of nesting birds declined from 84.6 to 73.1 pairs per 100 acres. Species composition changed but the number of species remained about the same. The two major habitat changes were maturation of the forest and browsing by the increasing white-tailed deer population.—George A. Hall.

Island Africa. By Jonathan Kingdon. Princeton Univ. Press, Princeton, New Jersey. 1990:287 pp., many colored and black & white drawings. $39.50.—The subtitle of this attractive book, "The evolution of Africa's rare animals and plants," explains the book's rationale. A number of ecological islands, both offshore and inland, are discussed from an historical standpoint, detailing these "islands" as centers of evolution and of endemism. The book is copiously illustrated with both colored and black-and-white drawings. Although all vertebrate taxa, and some invertebrates, are discussed, there are many examples of birds.—George A. Hall.

Managing Waterfowl Populations. Edited by G. V. T. Matthews. Special Publication No. 12, International Waterfowl and Wetlands Research Bureau, Slimbridge, Gloucester, England. 1990:230 pp., numerous black-and-white maps and charts. £12.—The IWRB held a symposium in Astrakhan, USSR, in October 1989, and the Proceedings are now at hand. While there are contributions from North America and western Europe, the majority of the 54 papers report on waterfowl in the U.S.S.R. There are also a few papers from Africa, China, and South America. These papers are categorized under the headings: Distribution and Status of Waterfowl; Hunting Kill Statistics; Hunting Management; Controlling Factors other than Hunting Kill; Conservation of Threatened Species; and General Management Strategies. The international flavor makes this a useful publication for waterfowl biologists.—George A. Hall.

Cold Weather Movements of Waterfowl in Western Europe. By S. C. Ridgill and A. D. Fox. Special Publication No. 13, International Waterfowl and Wetlands Research Bureau, Slimbridge, Gloucester, England. 1990:89 pp., many maps and graphs. £10 (£1.50 postage and packing).—The cold weather movements of nine common species were investigated using banding data and the International Waterfowl Census counts.—George A. Hall.

The following two publications can be obtained free of charge from the Publications Unit, U.S. Fish and Wildlife Service. 18th and C Streets NW, Room 130 Arlington Square Building, Washington, D.C. 20240.

North American Breeding Bird Survey Annual Summary, 1989. By Sam Droege and John R. Sauer. U.S. Fish and Wildlife Service Biological Report 90(8), 1990:22 pp., 2 black-and-white figs.—G.A.H.

Tests of a Habitat Suitability Model for Black-capped Chickadees. By Richard L. Schroeder. U.S. Fish and Wildlife Service, Biological Report 90(10), 1990:8 pp. 4 black-and-white figs.—G.A.H.

ORNITOLOGIA NEOTROPICAL. Edited by Karl-L. Schuchmann. The Neotropical Ornithological Society. Vol. 1, No. 1–2, 1990:32 pp.—This first number of a new journal contains four papers, one in English and three in Spanish. Membership in the Society can be obtained by writing The Neotropical Ornithological Society, % Mario Ramos, World Wildlife Fund, 1250 24th Street NW, Washington, D.C. 20037. Annual dues are $35 ($15 for students and $25 in Latin American countries).—G.A.H.

REPOSITORY FOR FROZEN TISSUES

We wish to publicize the existence of the Collection of Frozen Tissues at the LSU Museum of Natural Science. The Collection is supported by NSF and LSU as a service to the research community. It contains tissue samples of over 30,000 vertebrate animals preserved at −70°C. We are committed to proper curation and research use of frozen tissue samples. Although our freezer space is limited, we would like to offer our collection as a repository for personal research collections or orphaned collections that are no longer needed but are still valuable to the research community, and are perhaps occupying needed freezer space. Materials donated to the Collection become the property of the Collection (our policy on Collection use is available upon request). If you have materials you wish to donate or would like to use materials in the Collection please contact Dr. Robert M. Zink, Curator, Collection of Frozen Tissues, Museum of Natural Science, Louisiana State University, Baton Rouge, LA 70803.

1991 NABS RESEARCH AWARDS

The North American Bluebird Society is pleased to announce the presentation of the eighth annual research grant awards. The 1991 recipients are as follows:

BLUEBIRD GRANTS

Mark T. Stanback, Hastings Natural History Reservation
The Betty H. McIlwain Award
Topic: Factors Affecting Eastern Bluebird Reproductive Success in the Southeastern United States
Dr. Harry W. Power, Rutgers University
Topic: Male Parental Investment and the Threat of Cuckoldry in Mountain Bluebirds

STUDENT GRANTS

John P. McCarty, Cornell University
The James L. Williams Award
Topic: The Interaction of Environmental Conditions and Patterns of Nestling Energetic Requirements in Determining Reproductive Success of the Tree Swallow
Linda A. Whittingham, Queens University
Topic: How Should Male Parental Care Change with Decreasing Certainty of Paternity?

GENERAL GRANTS

Dr. Ian G. Warkentin, Smithsonian Institution
Topic: Winter Ecology of Prothonotary Warblers—Foraging Behavior and Habitat Use

NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANTS—1992

The North American Bluebird Society announces the ninth annual grants in aid for ornithological research directed toward cavity nesting species of North America with emphasis on the genus *Sialia.* Presently three grants of single or multiple awards are awarded and include:

Bluebird Research Grant. Available to student, professional or individual researcher for a suitable research project focused on any of the three species of bluebird for the genus *Sialia.*

General Research Grant. Available to student, professional or individual researcher for a suitable research project focused on a North American cavity nesting species.

Student Research Grant. Available to full-time college or university students for a suitable research project focused on a North American cavity nesting species.

Further guidelines and application materials are available upon request from:

Kevin L. Berner
Research Committee Chairman
College of Agriculture and Technology
State Univ. of New York
Cobleskill, New York 12043

Completed applications must be received by December 2, 1991; decisions will be announced by January 15, 1992.

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See Wilson Bulletin, 103:163–164, 1991 for more detailed "Information for Authors."

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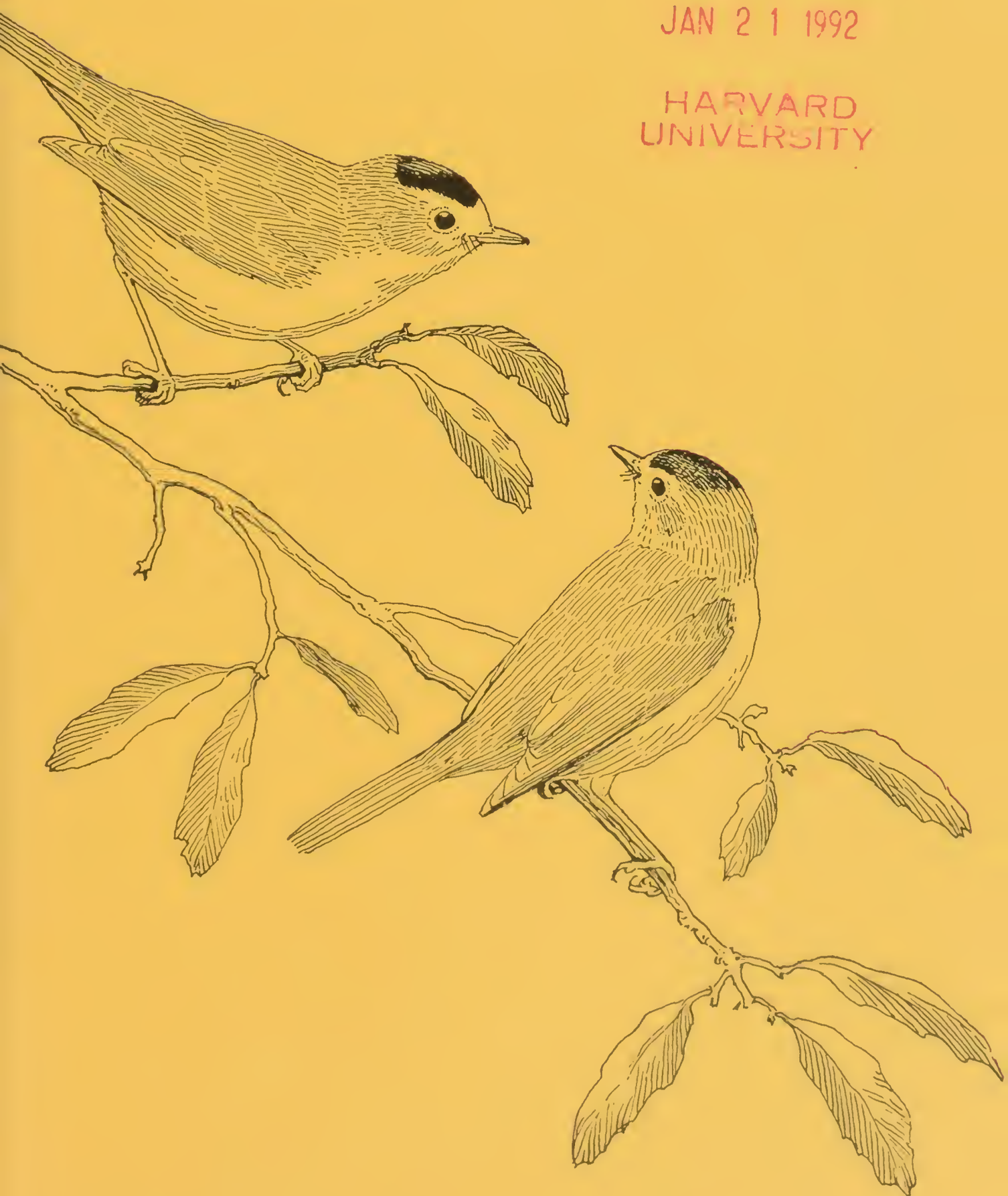

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NOTES ON THE BEHAVIOR AND ECOLOGY OF THE RED-COTINGAS (COTINGIDAE: *PHOENICIRCUS*)

PEPPER W. TRAIL[1] AND PAUL DONAHUE[2]

ABSTRACT.—The two species of red-cotingas, *Phoenicircus,* are little-known birds with a patchy distribution in the rain forests of northern and central South America. We observed the foraging, displays, and vocalizations of the Guianan Red-Cotinga (*P. carnifex*) in Suriname and of the Black-necked Red-Cotinga (*P. nigricollis*) in northeastern Peru. Males of both species formed small, low-density leks. Almost all display occurred in the first hour after dawn, after which the birds dispersed and were rarely observed. Direct interactions between displaying males were infrequent, and male–male spacing at the lek appeared to be mediated through calling. Display consisted of repeated calling and horizontal flights between perches 5–15 m up in the understory. Display flights are often accompanied by mechanical whistling sounds. Although we observed female visits to the lek, no copulations or obvious pre-copulatory behaviors were seen. In courtship and vocalizations, as in morphology, red-cotingas exhibit characters of both manakins and cotingas. *Received 19 Feb. 1991, accepted 28 May 1991.*

The red-cotingas, genus *Phoenicircus,* are two closely related species inhabiting the lowland rain forests of northern and central South America. In both species, the male has a brilliant scarlet crown, breast, rump, and tail. The sides of the head, throat, back, and wings are black in male Black-necked Red-Cotingas (*P. nigricollis*) (see Frontispiece) and dark brown in male Guianan Red-Cotingas (*P. carnifex*). The females of both species are duller, with olive brown wings and backs and pale rosy un-

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COLOR PLATE

Male Black-necked Red Cotinga (*Phoenicircus nigricollis*) on a display perch in the rain forest of eastern Peru. Painting by Paul Donahue.

derparts. The Black-necked Red-Cotinga occupies upper Amazonia in Colombia, Ecuador, Peru, and Brazil, while the Guianan Red-Cotinga inhabits eastern Venezuela, the Guianas and lower Amazonian Brazil. Given the close similarity of the two forms, there is some question whether they are distinct species. The chief evidence for their being distinct is an area of possible sympatry along the southern tributaries of the Amazon, particularly the Rio Tapajós (Snow 1982).

The systematic position of *Phoenicircus* is uncertain. The outer and middle toes are united, as in manakins (Pipridae). Snow (1973) further suggested that the color of the plumage might indicate affinities with the manakins. Among the cotingas, *Laniisoma* also exhibits united toes as well as another character of *Phoenicircus,* modified seventh primary feathers. However, in *Phoenicircus* the seventh primaries are shortened and strongly recurved, while in *Laniisoma* they are slightly elongated and attenuated at the tip. Sclater (1888, cited in Snow 1973) linked *Phoenicircus* with the cocks-of-the-rock, *Rupicola,* apparently based on body color, the anterior crest (slight in *Phoenicircus,* extremely exaggerated in *Rupicola*), and the modified primaries (seventh in *Phoenicircus,* tenth in *Rupicola,* and differently shaped in the two genera). Snow (1973, 1982) concluded that in the absence of strong evidence to the contrary, it was best to retain *Phoenicircus* as an isolated genus within the Cotingidae.

The ecology and behavior of both species of red-cotingas are virtually unknown (Snow 1982). In this paper, we summarize observations on the diet, display, and vocalizations of both *P. nigricollis* and *P. carnifex* made during the course of other studies in Peru and Suriname.

STUDY AREA AND METHODS

Trail observed a small population of *P. carnifex* from December 19, 1985 to March 17, 1986 at the Brownsberg Nature Reserve, Brokopondo Province, Suriname. This 6000-ha reserve (4°53′N, 55°13′W) is located 130 km south of Paramaribo on the western shore of the Brokopondo Reservoir. The study area was at the northern end of the reserve's Mazaroni Plateau (elev. 500 m).

P. carnifex is rare and local in Suriname. Aside from Brownsberg and vicinity, it has been reported only from the Kayser Mountains in southern Suriname (Haverschmidt 1968). Trail never recorded the species in 24 months of fieldwork in the lowland rain forests of the Raleigh Falls-Voltzberg Nature Reserve (elev. 20 m), approximately 125 km WSW of Brownsberg.

Donahue observed *P. nigricollis* on 10 days between November 29, 1988 and January 11, 1989 at the ExplorNapo camp of Explorama Tours, Dpto. Loreto, Peru (3°15′N, 72°55′W). This camp (elev. 140 m) is located approximately 72 km NE of Iquitos, along Sucusari Creek, a left bank tributary of the Rio Napo. Donahue has not encountered the bird elsewhere in the course of repeated visits to the species' range in NE Peru and E Ecuador.

It is worth noting that neither of us has seen or heard red-cotingas more than 1 km from the display areas at either of our study sites. Localized distributions and small population sizes appear to be typical of both species of red-cotingas across their entire range (Snyder 1966, Hilty and Brown 1986).

Observations of displaying birds were made using 8× or 10× binoculars and a 15× spotting scope. Vocalizations were recorded on cassette tape, using Sony and Marantz recorders and Sennheiser directional microphones. Analysis of vocalizations was carried out using a Kay DSP-5500 Sonagraph.

RESULTS

Measurements.—One adult male *P. carnifex* was mist netted two times, on January 24 and February 15, 1986. The wing length was 94 mm; culmen 10.5 mm; gape width 18.5 mm; weight 77 g (Jan. 24) and 78 g (Feb. 15). All feathers appeared new, and there was no molt on either date. Some of the soft part colors differed from those given in Snow (1982). The strikingly large eyes were dark brown; the bill was horn color; the gape was pale yellow; and the legs were pinkish-flesh in color. The soft part colors of *P. nigricollis* are similar, but the bill is yellow ochre.

Characteristics of Phoenicircus leks.—The only published description of red cotinga courtship indicates that males of *P. nigricollis* display in groups of up to 12 individuals and that these groups may move widely (Olalla 1943, cited in Snow 1982). Displaying male Black-necked Red-Cotingas observed in Brazil were described as very tame (Olalla 1943, cited in Snow 1982), but we found both species to be difficult to approach closely.

Fig. 1 illustrates typical postures of male *P. nigricollis*. Drawings A, B, and G show birds in relaxed perching postures; drawings C, F, H, and I illustrate different states of alertness. Display postures are shown in drawings D, E, J, K, and L; these are described in more detail below. Note that the tail is often twisted slightly to the side both during perching (Fig. 1F) and calling (Fig. 1D, E). This emphasizes the conspicuous rump.

The display area of *P. nigricollis* at ExplorNapo was in terre firme forest, along a low, wide ridge. All displays and calling took place within an area measuring approximately 300 × 150 m, with the most intense activity centered in an area about 75 × 150 meters. Although the wide spacing and frequent flights of the males made accurate counts difficult, a total of 6–10 males probably displayed regularly in this area. Display and foraging took place in the understory from 8–15 m above the ground.

At Brownsberg, all observed *P. carnifex* displays occurred in an area measuring approximately 100 m × 50 m. The forest in this area was characterized by scattered tall emergent trees reaching a height of 40 m, a canopy at approximately 30 m, a well-developed understory level of small trees at about 10–15 m, and little growth beneath this understory. The red-cotingas occupied the understory level, typically displaying and foraging at a height of 8–12 m. A lek of eight male Capuchinbirds (*Perissocephalus tricolor,* Cotingidae) occupied the lower canopy in this same site, at a height of 15–25 m.

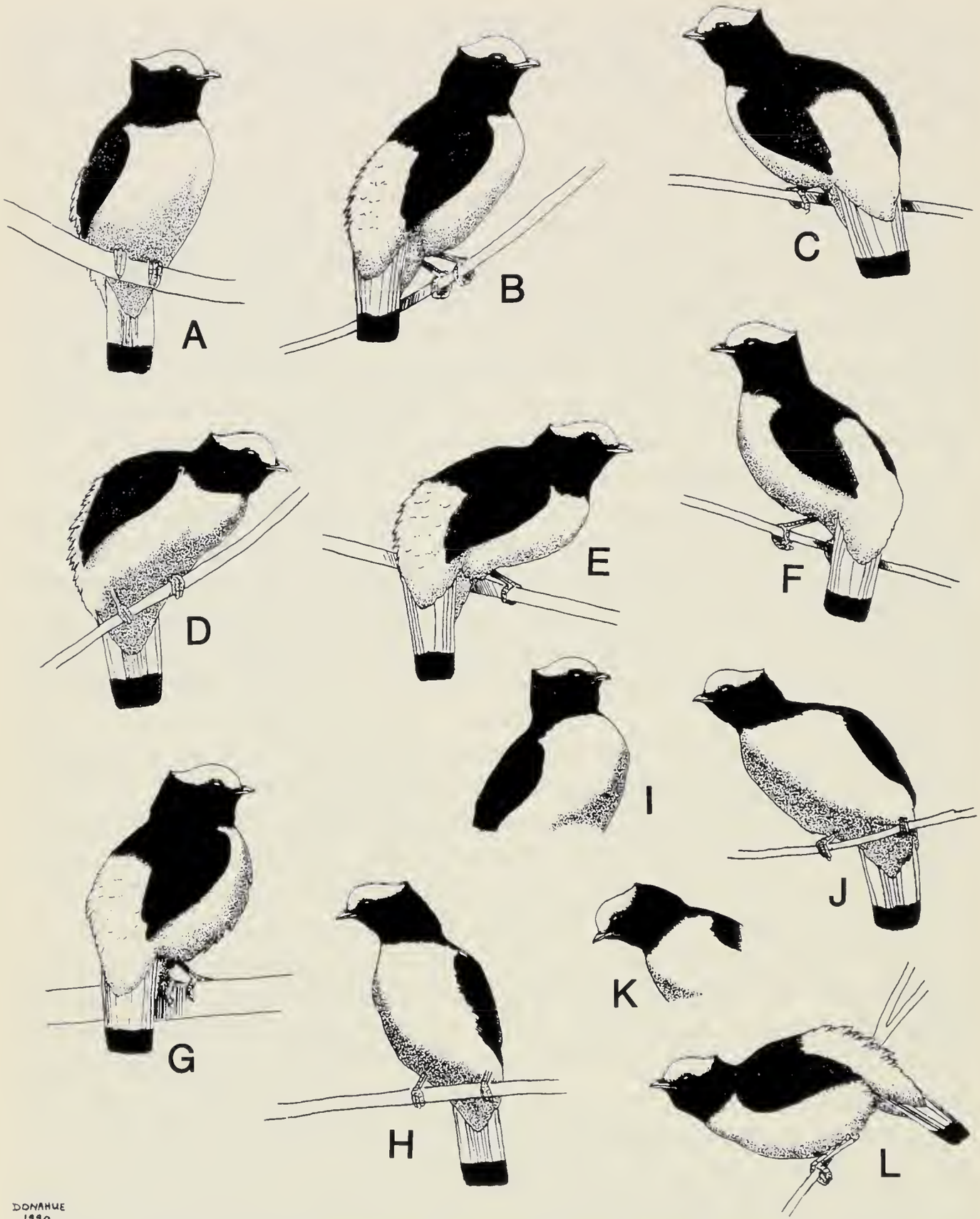

FIG. 1. Postures of male *Phoenicircus nigricollis,* based on field sketches. A, B, G. Relaxed perching. C, F, H, I. Various alert postures, ranging from low (C) to high (H) intensity. D, E, L. Bowing postures of calling males. J, K. Male between calls, showing head-bobbing.

On most days, two male red-cotingas displayed in the area. One male was captured and color banded on January 24 and was resighted repeatedly through the remainder of the observation period. The other male was unbanded but could be individually recognized by a horizontal band of lighter feathers on his upper breast. A third male was observed calling infrequently in this area (less than one day per week).

During our one to three month observation periods, males displayed daily within adjacent, largely exclusive ranges, and did not appear to display elsewhere. The display ranges were very small in relation to the similar surrounding habitat, and contained no concentration of resources used by visiting females. Although there were some fruiting trees in the display areas, the same tree species appeared widespread in the surrounding forest. These characteristics of the display sites and the display behavior of male red-cotingas fulfill the criteria for lek behavior (Bradbury 1981).

Male–male interactions at the lek.—In *P. carnifex,* the two regular males maintained adjacent, slightly overlapping regions of display activity, typically remaining at least 20 m apart. At this distance, they were frequently out of visual contact but in continual auditory contact. The display area of the banded male was elliptical, measuring approximately 60 m × 20 m; that of the unbanded male was more nearly circular, measuring about 30 m in diameter. The display areas of the male *P. nigricollis* appeared to be in this same size range, or slightly larger.

Overt aggression between male red-cotingas was observed only once. This occurred at the *P. carnifex* lek outside the usual display area of either resident male, but nearer the unbanded male's range. The birds were perched in adjacent saplings, only 4 m apart. For 10 min, the males made occasional short flights (with wing-whistling, described below) but gave no calls and engaged in no direct interactions. Then the banded male flew to within 2 m of the other bird, who promptly supplanted him with a strike or near-strike. Shortly thereafter, the banded male flew out of sight in the direction of his normal display range. He gave an advertising call from his new location (at least 20 m away), which the unbanded male immediately answered. When Trail then gave an imitation of this call, the unbanded male responded by flying assertively around the area, looking for the source. On other occasions, these males were observed feeding together without aggression at fruiting trees near the lek.

Descriptions of courtship displays and vocalizations.—The display of both *P. carnifex* and *P. nigricollis* occurred almost exclusively during the first one to two hours after first light, with only occasional calling later in the day. During 13 observation days on *P. carnifex* from December 24,

1985–February 4, 1986, the mean time of the first call was 05:48 h (range 05:39–05:55). The mean time of the first call for *P. nigricollis* was almost identical: 05:42 h (range 05:36–05:46, N = 4 mornings). This was approximately 15 min after first light in the forest interior. Display activity appeared to be more intense on sunny mornings than when there was overcast. On most days, calling continued actively until 06:30–07:00 h, after which the males were rarely seen.

In both species, this dawn period was usually the only bout of display, although on some days there was sporadic calling at other times, particularly in the late afternoon. If one male began calling after dawn, the other male usually returned to his display area and joined in. This pattern is presumably the basis for the statement that the group of displaying males in *P. nigricollis* is "called up" by one individual (Olalla 1943, cited in Snow 1982). The brief daily display of *Phoenicircus* contrasts with the more extensive display of most other lekking cotingas and manakins and may help to explain the paucity of observations on red-cotingas.

All the displays that we observed were associated with the production of vocalizations and mechanical noises. The most common vocalization of *P. carnifex* was the advertising call (Fig. 2A) which can be rendered as "pee-chew-eet." This call was always the first vocalization given at dawn. The preferred calling perches were small horizontal branches or lianas, free from foliage, 8–10 m up. Each male called from at least a dozen perches within his range and did not have obvious favorites.

During bouts of "pee-chew-eet" calling, the males typically maintained an upright posture with their tails straight down and their scarlet rump feathers fluffed out and very conspicuous. They also erected their short crown feathers, which then partially covered the base of the bill. As they produced the call, the males pulled their heads back in a pumping motion. The interval between "pee-chew-eets" during calling bouts averaged 16 sec (range 4–44 seconds, N = 59).

The advertising call of *P. nigricollis* is a loud note which can be rendered as "whea"; this was often preceded by a soft "wur" note (Fig. 3A). "Whea" calls were always the first vocalization to be heard at dawn. They were sometimes given in series, with either increases or decreases in volume from the first to last call. During intense calling, the "whea" sometimes became distinctly two-syllabled: "whee-ah," with the accent on the first syllable.

During calling, the males bowed forward on their perches, with conspicuously ruffled rump feathers (Fig. 1D, E, L). Between calls, the male remained in a slightly bowed posture and commonly performed a rapid forward head bobbing or bowing (Fig. 1J, K). This was similar to the head-pumping of *P. carnifex* but did not accompany the production of the call itself. Each male appeared to have 3–5 favorite calling sites within

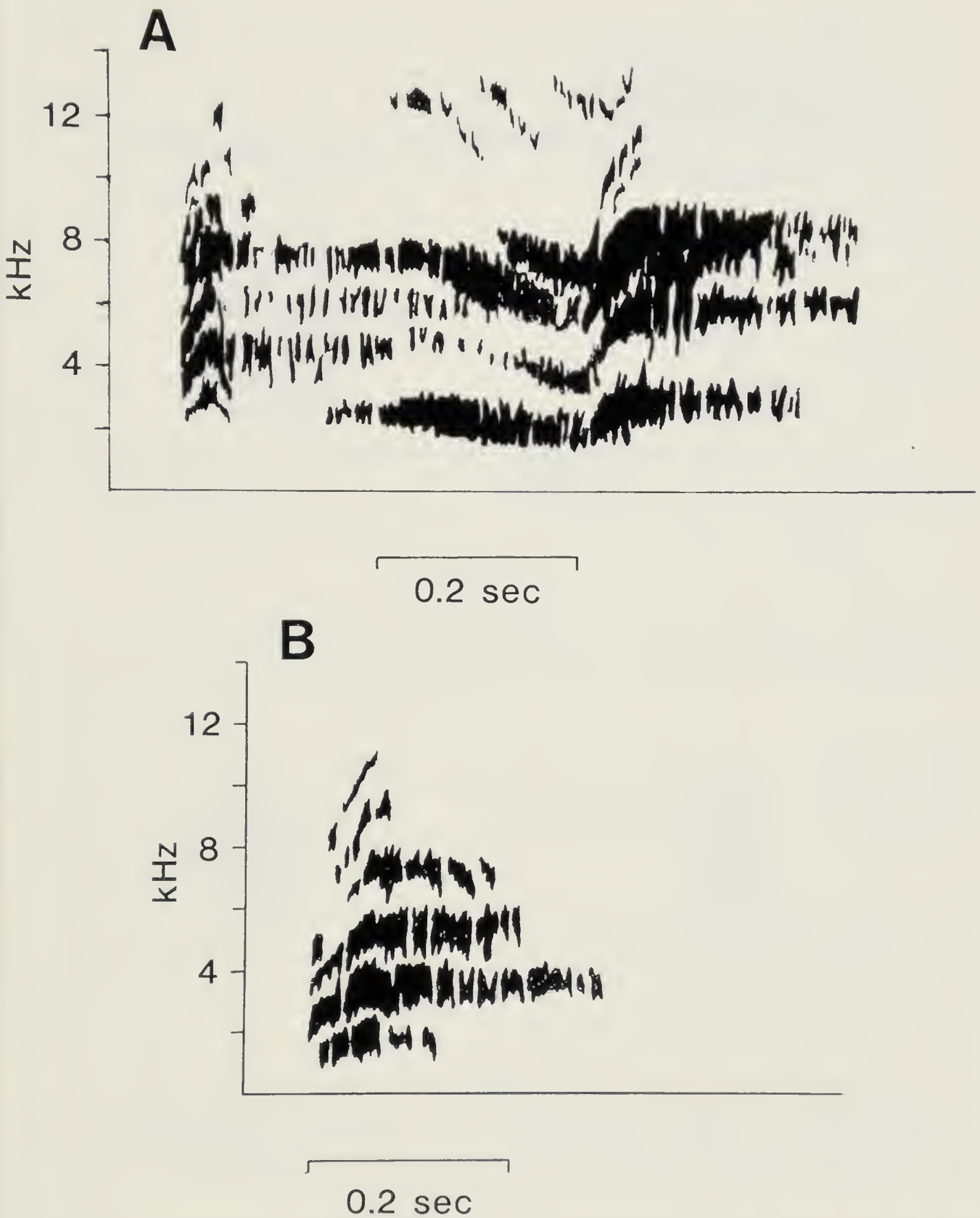

FIG. 2. Vocalizations of *P. carnifex*. A. The "pee-chew-eet" advertising call. B. The "wheep" call, which is given in contexts of arousal and alarm. See text for further information.

his display area. Horizontal sections of hanging lianas were the overwhelmingly preferred calling perches.

The most obvious display in both species of red-cotingas was the horizontal flight display. Males flew rapidly between calling perches 6–20 m apart, swooping up to land on the new perch. During all display flights,

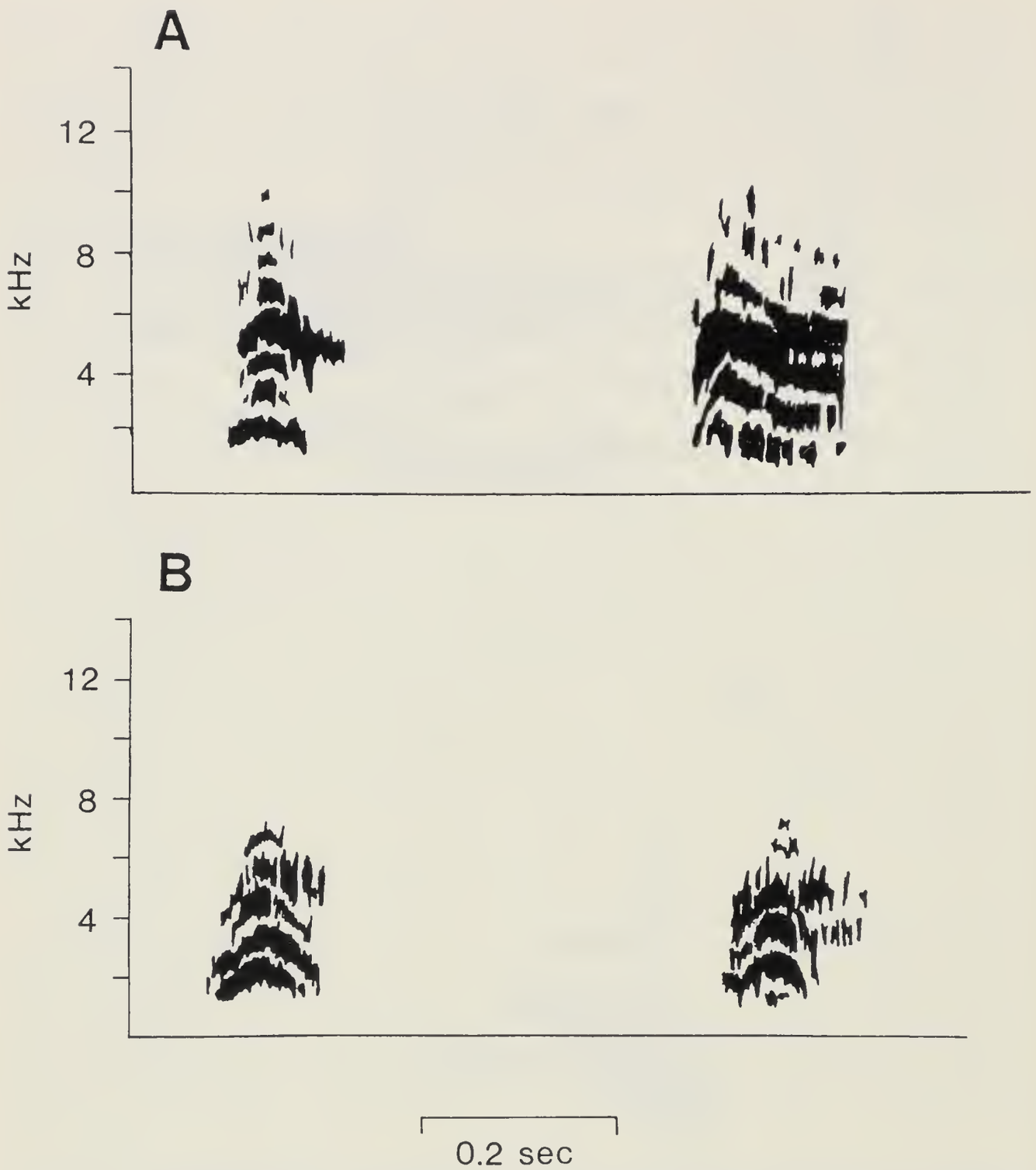

FIG. 3. Vocalizations of *P. nigricollis*. A. The advertising call: a quiet "wur" followed by a loud "whea." The "whea" was frequently given without the introductory note. B. Two examples of the "yip" arousal or alarm call. See text for further information.

the males in both species produced a characteristic mechanical sound, presumably with their modified seventh primary feathers (illustrated in Snow 1982). This was a two-part ringing sound, recalling a rapid pair of cricket calls (Fig. 4).

Male *P. carnifex* frequently produced a high-pitched whistle vocalization (Fig. 4) as the male swooped onto a perch at the end of a flight display.

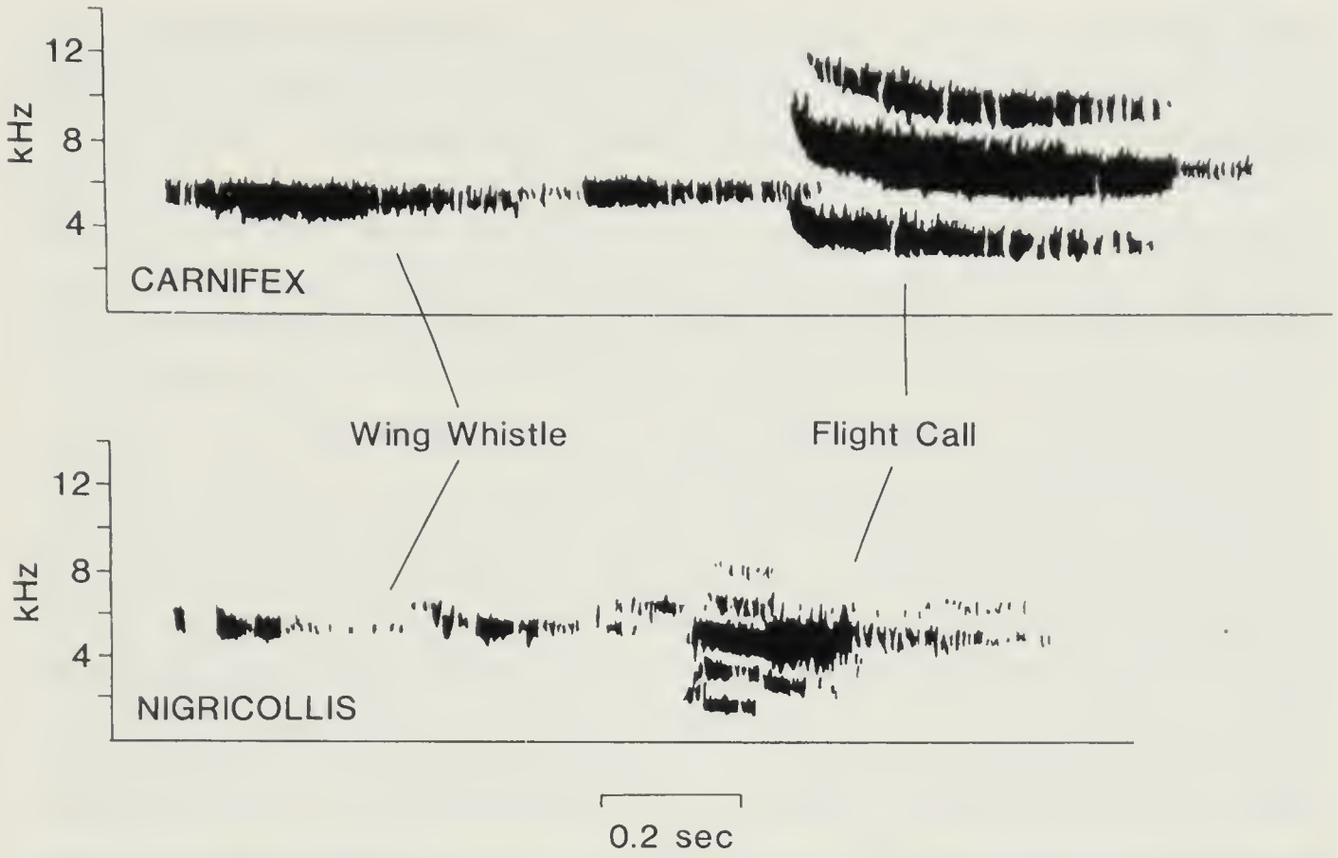

FIG. 4. Flight sounds of *Phoenicircus*: mechanical wing whistles followed by flight calls. A. *P. carnifex*: wing whistle followed by flight whistle. B. *P. nigricollis*: wing whistle followed by abbreviated version of the "whea" call given in flight.

This whistle was never given independent of flight display, but the flight display was sometimes performed without the whistle call. When the flight whistle vocalization was given, it followed the mechanical wing whistle, never preceded it.

Male *P. nigricollis* apparently did not call in flight as frequently as did *P. carnifex*. However, they did sometimes produce an abbreviated version of the "whea" call at the end of a display flight, following the mechanical wing whistle (Fig. 4). This was much lower-pitched than the *P. carnifex* flight whistle, and sounded more like a squawk than a descending whistle.

The third *Phoenicircus* vocalization was a short, loud monosyllable, which sounded like "wheep!" (in *P. carnifex*) or "yip!" (in *P. nigricollis*). The versions of this call produced by the two species were similar, although the *P. carnifex* version was higher-pitched (Figs. 2B and 3B). Unlike the advertising and flight calls, the "wheep" call was given by both male and female red-cotingas. It appeared to signal a high degree of arousal or alarm, as it was given both in response to human disturbance and during female visits to the display area. In such situations, long series of "wheep" calls were sometimes given without any other vocalizations. This call was reminiscent of the "hey" alarm call of another cotinga, the Guianan Cock-of-the-Rock, *Rupicola rupicola* (see Trail 1987, Fig. 2).

The final sound produced by *P. carnifex* was the wing buzz. This two-

part mechanical sound was short and loud, very different from the high-pitched wing whistle. Trail heard the wing buzz very rarely and saw it being produced only once. On this occasion, three male red-cotingas were in close proximity at a fruiting tree on the edge of the display area. One male made a short (≤2 m) flight upward at a 45° angle, during which this two-part buzz was produced. No further details were seen, and the significance of this sound remains unknown. Male *P. nigricollis* were never heard to produce a loud wing buzz. Given the rarity of this sound in *P. carnifex,* however, it may still be recorded in *P. nigricollis.*

Male–female interactions.—Drably colored *P. carnifex* were observed at the Brownsberg lek on five occasions. These were probably all females. The plumage of young male red-cotingas resembles that of females but is brighter (Snow 1982); no such intermediate plumages were seen. During these visits, the males concentrated their activity in the vicinity of the female, and the rates of "pee-chew-eets" and especially flight displays and flight whistles increased. In the absence of females, the ratio of "pee-chew-eets" to flight whistles was about 5:1, but during female visits this ratio dropped to approximately 2:1. This supports the interpretation of "pee-chew-eets" as advertising calls, with display flights and flight whistles representing more directed courtship behavior.

Despite their increased rates of calling and flight displays, male red-cotingas did not attempt to intercept or perch adjacent to females visiting the display area. We recorded no novel displays or calls associated with female visits, and observed no direct courtship interactions or matings. Female red-cotingas either simply passed through, or stopped for a few minutes to feed on fruits in the display area. They frequently gave "wheep" calls, but we were unable to determine whether these were given to attract males, in response to the males' displays, or in response to our presence.

Female visits to the *P. nigricollis* lek at ExplorNapo Camp were not observed. Periodically during observations, the rate of "whea" calling would increase dramatically. This presumably signalled the approach of a female, but the large distances between males and the wariness of the birds precluded confirmation.

Behavior away from display sites.—During the course of studies at Brownsberg, Trail and assistants spent much time walking through the forests of the northern Mazaroni Plateau, an area of approximately 4 km^2. We rarely heard red-cotingas away from the display area (always giving "wheep" calls) and sighted them only once. On this occasion we located two female-plumaged red-cotingas giving a series of "wheep" calls, at least 0.5 km from the display area. These birds remained 4–5 m apart, but they moved together, apparently foraging for fruit 6–10 m up in the thick understory foliage. An unbanded male was also present, actively flying around the area with wing-whistles, but without giving "pee-chew-

eet" or "flight whistle" calls. This male never directly interacted with the females but remained in their vicinity. He had a pale ring of feathers on his breast and may have been the same individual as the similarly marked unbanded male at the display area.

P. nigricollis were observed away from the lek only twice, despite extensive walking by Donahue over the surrounding 4–5 km^2 of forest. Both these observations were brief glimpses and occurred within approximately one-half kilometer of the lek.

Observations on feeding.—Red-cotingas appear to be completely frugivorous, with recorded food items from the families Palmae (*Euterpe*), Moraceae (*Ficus*), and Passifloraceae (Snow 1982). At Brownsberg, *P. carnifex* was observed feeding on the fruits of Myrtaceae (*Eugenia*), Guttiferae (*Clusia*), Melastomataceae (*Miconia*), and Lauraceae (genus unidentified). At ExplorNapo camp, *P. nigricollis* was observed feeding on the fruits of Meliaceae (*Trichilia*).

Moermond and Denslow (1985) have suggested that red-cotingas may rely on hovering and stalling flight maneuvers to gather fruits, based on the short, highly slotted wings and high wing loading of these species. In stalling, a bird uses a steep wing attack angle stop briefly in front of the fruit, which is then seized. Twenty-one fruit captures by *P. carnifex* were observed. Fruits were taken in flight in 12 cases, using the following methods: snatch (5 times), stall (4 times), and hover (3 times). In the remaining 9 foraging observations, red-cotingas picked fruit from a perched position. The picked fruit was a berry in a panicle in seven cases and a drupe in the other two cases.

All observations of feeding in *P. carnifex* took place at the lek and its immediate vicinity. Males typically made between one and three fruit captures, and then returned to display perches. Feeding was usually solitary, although the resident males sometimes fed together. Red-cotingas were never seen accompanying the mixed species flocks that fed on fruit in the forest canopy at Brownsberg. The observation, described above, of three red-cotingas travelling together away from the lek suggests that the birds sometimes forage socially, although feeding was not observed.

On the only occasion when feeding was observed in *P. nigricollis*, a male and a female were seen feeding on the fruits of a *Trichilia* tree located near the center of the lek. Feeding with them in the same tree were Black-spotted Barbet (*Capito niger*), Lawrence's Thrush (*Turdus lawrencii*), and White-tailed Trogon (*Trogon viridis*).

DISCUSSION

Our observations support the traditional classification of *P. carnifex* and *P. nigricollis* as separate species. Although the displays are similar, the vocalizations are distinct. If these species do come into contact south

of the Amazon, it is likely that the differences in their lek behavior would be sufficient to prevent interbreeding. Given the apparent affinities of *Phoenicircus* with both the cotingas and the manakins, it is of particular interest to compare the courtship displays of red-cotingas with those of other members of these two families. The evolution of displays in manakins has been extensively discussed (Snow 1963, Sick 1967, Prum and Johnson 1987), and Snow (1982) has reviewed the information available on courtship behavior in the cotingas (see also Trail 1985, Bierregaard et al. 1987).

In vocalizations and displays, as in morphology, *Phoenicircus* recalls both manakin and cotinga species. The posture of a male *P. carnifex* giving the "pee-chew-eet" call, with fluffed rump and erect crown, resembles that of the cocks-of-the-rock (*Rupicola*), a similarity noted by Robert Ridgley (cited in Hilty and Brown 1986). The advertising calls, and particularly the accompanying head-pumping motion in *P. carnifex,* recall another group of cotingas, the pihas (*Lipaugus*). The flight display resembles that of the *Pipra* manakins, particularly *P. erythrocephala* (Snow 1962a, Lill 1976), while the wing buzz is strikingly like sounds produced by the manakins of the genus *Manacus* (Snow 1962b, Lill 1974). The wing whistle accompanying the red-cotinga flight display is more unusual, but recalls the sounds made by male Guianan Cock-of-the-Rock in flight. In the cock-of-the-rock, however this sound (produced by elongated tips on the tenth primaries) is not part of a special flight display. Finally, the alarm call of *Phoenicircus* resembles that of *Rupicola.*

The blend of cotinga and manakin courtship behaviors exhibited by red-cotingas emphasizes the closeness of these families. Observations of precopulatory behavior and mating in *Phoenicircus* may provide further insight into the affinities of this fascinating genus. As in the manakins in which acrobatic flight displays are important elements of courtship (especially *Pipra* and *Chiroxiphia*), male *Phoenicircus* are significantly smaller than females (Snow 1982). This suggests that the as-yet-unreported precopulatory displays of male red-cotingas may involve more elaborate flight maneuvers than those we observed.

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dedicated to David and Barbara Snow in admiration of their pioneering field studies of cotinga behavior and ecology.

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COLOR PLATE

The frontispiece painting by Paul Donahue has been made possible by an endowment established by George Miksch Sutton.

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REPEATABILITY OF CLUTCH SIZE IN HOUSE WRENS

E. Dale Kennedy[1] and Douglas W. White[1]

Abstract.—Theories of clutch-size determination have focused primarily on first broods or on seasonal trends in clutch size. High repeatability between the sizes of first and second clutches could be expected because of individual genetic, vigor, and environmental differences. We examined the repeatability of clutch size in individual House Wrens (*Troglodytes aedon*) both within and across years using data collected between 1926–1937 by Kendeigh, Baldwin, and others. Contrary to expectation, repeatability of clutch size in first and second clutches within a year was low ($r_I = 0.10$) and only about one-third that of first or second clutches among different years ($r_I = 0.27$ or 0.30, respectively). Despite modest repeatability in clutch size, no significant correlation existed between number of fledglings in successful first broods and clutch size of second broods ($r = 0.006$). Clutch-size repeatability was associated with female identity and not nest box site, suggesting that differences in individual clutch size did not result from occupation of differentially suitable breeding territories. Estimates of heritability of clutch size were limited due to small numbers of fledglings that returned to natal study sites to breed; however, the estimate of heritability of clutch size was greater for mother-son combinations ($h^2 = 0.48$) than for mother-daughter combinations ($h^2 = 0.21$). *Received 11 Oct. 1990, accepted 18 June 1991.*

Clutch size in birds is controlled by a combination of genetic, ontological, and environmental factors. Theories of clutch-size determination have focused on first broods or on seasonal trends in clutch size. For birds that rear more than one brood in a season, the question of what is the most productive clutch size for an individual (sensu Lack 1947, 1966) may become complicated if clutch size (or fledging success) varies independently or inversely between one brood and the next (see Murphy and Haukioja 1986 for a review).

Repeatability (r_I) is the correlation between repeated measurements, separated in space or time, of a character from the same individual (Falconer 1981:127). Both environmental and genetic factors may contribute to repeatability, according to the formula:

$$r_i = (V_G + V_{Eg})/V_P,$$

where V_G represents genetic variance, V_{Eg} represents general environmental variance, and V_P represents total phenotypic variance (Falconer 1981:127). Repeatability sets an upper limit to heritability (h^2; Falconer 1981:127), the proportion of total phenotypic variance that is attributable to additive genetic variance ($h^2 = V_A/V_P$; Falconer 1981:148).

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Repeatability of clutch size is a measure of individual consistency in reproductive effort (Boag and van Noordwijk 1987, Lessells and Boag 1987). Given the potential heritability of clutch size and the potential for intraseasonal continuity in breeding circumstances, we would expect high repeatability in first- and second-clutch sizes within a breeding season, at least in comparison with repeatability in different years.

Alternatively, if strong trade-offs existed between first and second reproductive efforts (McGillivray 1983, Slagsvold 1984, Lindén 1988), intraseasonal repeatability could be low or negative because of energetic or time constraints.

Here we examine repeatability of clutch size in individual female House Wrens (*Troglodytes aedon*) both within a breeding season and across years. House Wrens are cavity nesters that are often double-brooded, generally laying first clutches of 4–8 eggs and second clutches of 3–7 eggs.

METHODS

Breeding biology of House Wrens was studied by S. P. Baldwin, S. C. Kendeigh, and their coworkers at the Baldwin Bird Research Laboratory in Gates Mill, Ohio, between 1919 and 1940. The study area and field methods were detailed by Baldwin and Bowen (1928) and Kendeigh (1941a).

Field notes of the Baldwin Bird Research Laboratory are in the library of the Bird Division, Museum of Zoology, Univ. of Michigan. Volumes for the years 1926–1937, the 12 years of most active research, were lent to EDK, who recorded for each nest the band numbers of adults, the number of eggs laid, and the numbers and band numbers of fledglings.

Breeding females that had been banded as nestlings during the previous year or that had not been caught previously on the study sites were assigned an age of one year (see Kendeigh and Baldwin 1937; Kennedy 1991). For determining repeatability of clutch size, identifiable replacement clutches were omitted, as were double broods in which first or second clutch size data were lacking.

For each comparison listed in Table 2, repeatability was calculated as the intraclass correlation coefficient from a one-way analysis of variance (ANOVA; Lessells and Boag 1987). To preserve environmental and ontological sources of variation, no adjustments in clutch size were made for differences in female age, nest site, or study year (see Hailman 1986). In the determination of intraseasonal clutch-size repeatability, however, a misleading bias towards low values existed because modal clutch size declined progressively during the breeding season from seven eggs in May to four eggs in August (Kendeigh 1941b). To control for this temporal trend, second-clutch sizes were adjusted by adding the difference between the sample means for first- and second-clutch size, usually about one egg. Using this approach, intraseasonal repeatability values were similar to those found by simple correlation of first- and second-clutch sizes.

Heritability of first-clutch size was estimated for both mother-daughter and mother-son data. Heritability (h^2) was calculated as two times the slope of the regression of offspring clutch size on mother clutch size (Hailman 1986).

To determine whether a bird's cost of rearing a large first brood affected the size of her second clutch, we calculated a product-moment correlation coefficient for the number of fledglings in successful first broods and the number of eggs in second clutches.

RESULTS

In 412 cases, the number of eggs laid in consecutive first and second clutches of banded House Wrens was recorded between 1926 and 1937 near Cleveland, Ohio (Table 1). Observed double clutches were laid by 376 individual females (some females bred in several years). In 660 additional cases, first clutch size was recorded, but no second breeding attempt was observed.

Among double clutches, first clutches contained three to eight eggs (mean ± SD: 6.4 ± 0.8 eggs), and second clutches contained two to nine eggs (5.3 ± 0.9 eggs). Egg sets from females that laid single clutches within a year (6.2 ± 0.9 eggs) were fractionally smaller than first-egg sets from females that laid two clutches within a year ($t = -3.37$, df = 1,070, $P < 0.001$; some females were represented more than once in one or both categories). Second clutches occurred at a higher rate among females that laid the most common first-clutch sizes of six or seven eggs than among females that laid first clutches that were smaller or larger than usual (41% vs 28%, respectively). Overall, second clutches were observed for about 39% of female House Wrens.

Second-clutch size did not differ significantly among first-clutch sizes (Table 1; ANOVA, $F_{5, 406} = 2.22$, $P > 0.05$); thus, seasonal egg output (total eggs laid in the first plus second clutch) of double-clutched females increased from 10.4 to 13.8 eggs as first clutches increased from five to eight eggs.

Repeatability of clutch size in House Wrens in first and second clutches within years was low and only about one-third that of first or second clutches among different years (Table 2). The ANOVAs from which the repeatability values were derived were significant for intraseasonal clutch size for experienced females but not for females in their first breeding season (Table 2). Intraseasonal repeatability of clutch size was associated with female identity and not nest box site or male identity, suggesting that differences in individual clutch size did not result from continued occupation of differentially suitable breeding territories (Table 2).

We found no relationship between the number of nestlings that fledged from successful first broods and the number of eggs laid in second clutches ($r = 0.006$, df = 305, $P > 0.5$).

To test if poor correlation between sizes of first and second clutches resulted from offsetting trends among years, we examined each year separately. Significant correlation existed between first and second clutch size in only one of eleven years with adequate data (1928: $r = 0.50$, $P < 0.005$, N = 33; ten other years: $r = -0.09$ to 0.204, $P > 0.20$, N = 14 to 60).

Patterns of interseasonal repeatability suggested an upper limit on the heritability of clutch size of about 0.3. Based on mother and daughter

TABLE 1
FREQUENCY OF CLUTCH-SIZE COMBINATIONS IN HOUSE WRENS

Eggs in first clutch	Eggs in second clutch									Mean[b] ± SD
	0[a]	2	3	4	5	6	7	8	9	
3	5			1	1					4.5 ± 0.7
4	18				2	2				5.5 ± 0.6
5	88			6	13	11	3			5.3 ± 0.9
6	285		4	24	95	41	7	1	1	5.2 ± 0.9
7	237	1	6	16	81	68	12	3		5.4 ± 1.0
8	26			1	4	5	2	1		5.8 ± 1.1
9	1									

[a] No second clutch recorded.
[b] Mean second clutch size for each first clutch size (excluding 0).

first clutches, clutch size heritability (h^2) was 0.211 (N = 42). For mother and son first clutches, clutch size heritability was 0.48 (N = 61).

DISCUSSION

Both genetic and non-genetic factors may increase repeatability of clutch size within a breeding season. There is evidence for a genetic component to clutch size. Mother-daughter heritability of size of first clutches has been found for Great Tits (*Parus major*; Perrins and Jones 1974, van Noordwijk et al. 1980), Song Sparrows (*Melospiza melodia*), Mallards (*Anas platyrhynchos*), European Starlings (*Sturnus vulgaris*), Lesser Snow Geese (*Anser c. caerulescens*), and Red (Willow) Grouse (*Lagopus lagopus*;

TABLE 2
REPEATABILITY OF CLUTCH SIZE IN HOUSE WRENS

Comparison	*F* ratio (df)[a]	Repeatability
First and second clutches in one year[b]	1.232 (411, 412)*	0.104
Females one year old[b]	1.139 (293, 294)[ns]	0.065
Females more than one year old[b]	1.396 (117, 118)*	0.165
Any-age female at same nest box[b]	1.358 (145, 146)*	0.152
Any-age female, same box, same male[b]	1.493 (39, 40)[ns]	0.198
Same box, different female[b]	0.840 (96, 97)[ns]	−0.087
First clutches in different years	1.819 (157, 187)***	0.273
Second clutches in different years	1.917 (77, 90)**	0.299
Total eggs in first plus second clutches in different years	3.062 (36, 39)***	0.501

[a] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns = $P > 0.05$.
[b] Corrected for between-brood differences in mean clutch size, see Methods.

see reviews by Hailman [1986] and Boag and van Noordwijk [1987], but see Lessells and Boag [1987] for correction on heritability value of Lesser Snow Geese). Non-genetic differences that might increase repeatability of clutch size include (1) differences in vigor among females, (2) differences in breeding habitat, and (3) differences in breeding phenology. Some females are likely to be in better breeding condition, i.e., health or nutritional state, than others for non-genetic reasons and therefore should lay and rear larger numbers of offspring (see Price and Liou 1989 and included references). Females that nest and breed in "good" habitat should be able to lay and rear more offspring than those in "poor" habitat (Perrins and Jones 1974, Högstedt 1980). Females that begin breeding early in the season may have large first and second clutches relative to birds with later initiation dates. For this pattern to occur, clutch size must decline seasonally, and dates of first clutch initiation must be highly asynchronous; House Wrens display both traits (Kendeigh 1941a, b; 1963). Moreover, female vigor, habitat quality, and early breeding may be positively interrelated.

Intraseasonal repeatability in the number of eggs laid in first and second clutches of House Wrens was low, with $r_I < 0.17$ even when only sedentary or experienced females were examined (Table 2). Murphy (1978) found similar low intraseasonal repeatability in clutch size in House Sparrows (*Passer domesticus*; $r_I = 0.08$–0.12). Most House Wrens had second clutches of five or six eggs, regardless of the size of their first clutches. This result contradicts Kendeigh's suggestion (unpubl. field notes) that compensating variation in the sizes of first and second clutches produced a fixed seasonal total of ca 12 eggs. Expectations of high repeatability arising from female-to-female differences in genetics, vigor, habitat quality, or breeding phenology were also apparently contradicted by observed low intraseasonal repeatability.

In House Wrens, second clutch size was apparently independent of earlier brood-rearing effort because no significant correlation existed between second clutch size and the number of first-brood fledglings. Finke et al. (1987) found no differences in the frequencies of House Wrens that attempted second clutches or in average second clutch size among females rearing control, experimentally enlarged, or experimentally decreased first broods. In contrast, female Great Tits that laid second clutches were generally those that produced relatively few fledglings in first broods (van Noordwijk 1987, Lindén 1988), suggesting a trade-off.

In stark contrast to the within-year results, moderate repeatability ($r_I = 0.27$–0.50) existed in first clutch, second clutch, and season-total egg number for House Wrens in different years (Table 2). Moderate repeatability of first clutch size or seasonal egg total in different years has also

been found in Great Tits, Song Sparrows, Lesser Snow Geese (see review in Boag and van Noordwijk 1987), and Willow Grouse (Myrberget 1989; all $r_I = 0.23–0.51$) but not in Canada Geese (*Branta canadensis*; $r_I = 0.05$; see review in Boag and van Noordwijk 1987). Furthermore, heritability analyses suggested a significant genetic component to clutch size in House Wrens. However, the value for mother-son heritability of first clutches is likely an overestimate because it exceeds the value for repeatability of first clutches.

One potential interpretation for these seemingly conflicting results of low intraseasonal and high interseasonal repeatability is that first and second clutch sizes are influenced by separate genes. Such a genetic system seems unlikely in House Wrens, given the broad temporal overlap in breeding and the observation that repeatability of total eggs per season was greater than that for either first or second clutch size.

A second interpretation is that a tendency towards high intraseasonal correlation in clutch size may have been largely counterbalanced by a reproductive trade-off between early and late breeding periods. Under this scenario, two important biological phenomena (individual tendencies in clutch size and stress from reproduction) might go undetected because of their opposite impacts on the relationship between fledgling number in brood one and clutch size in brood two. The high repeatability observed for total eggs in first plus second clutches may have occurred because differences in reproductive stress were counterbalanced within this sum. In House Sparrows, high productivity in first broods suggested a high cost because it delayed the initiation of subsequent clutches and reduced subsequent fledgling success (McGillivray 1983). However, as in House Wrens, first-brood size in House Sparrows appeared unrelated to subsequent clutch size (McGillivray 1983), and intraseasonal repeatability in clutch size was low (Murphy 1978).

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SIBLING SPECIES OF GREENLETS (VIREONIDAE) IN SOUTHERN BRAZIL

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ABSTRACT.—As was already evident in the first collections of the early 1800s, the Rufous-crowned Greenlet (*Hylophilus poicilotis*) of southeastern Brazil to Bolivia is sympatric in southern São Paulo with the Gray-eyed Greenlet (*H. amaurocephalus*) of eastern Brazil. The two differ in color of eye, beak, and head, and have different songs. Reports of intergradation were based on failure to detect the important differences, in part due to lack of time (=support) for taxonomy. *Received 25 Sept. 1989, accepted 6 March 1991.*

Birds often are considered to be well-studied taxonomically, with new species appearing mainly in little-visited places. Taxonomy based on intensive studies of museum specimens has, theoretically, brought us to the point where there seems to be little more to do. In the last few years, however, careful study of vocalizations and biochemistry has shown that unrecognized sibling species lurk even in such well-studied regions as North America (Johnson and Marten 1988, Groth 1988), Central America (Stiles 1983), and southeastern Brazil (Willis 1988).

Johnson et al. (1988), studying proteins in vireos (Vireonidae), confirmed large electrophoretic differences in morphologically similar forms. They predicted that the family might prove to be taxonomically undersplit. Recently, studying vocalizations and observing birds in São Paulo State, Brazil, I found that *Hylophilus poicilotis*, the Rufous-crowned Greenlet, found from eastern Brazil to Argentina, Paraguay, and Bolivia, is actually two species, the southern *H. poicilotis* and the northern *H. amaurocephalus* (presently *H. p. amaurocephalus*). The two are sympatric and differ in voice, eye color, and plumage. They had been separated earlier, but Todd (1929) was the last person to defend separation before Hellmayr (1935) and Pinto (1944a) thought they found intermediate specimens.

Voice.—On 18 December 1982, visiting a small woodlot reserve of the state forestry institute at Mandurí (Fig. 1A), southern São Paulo, I was surprised to hear a simple "sweet-sweet-sweet-sweet-sweet" song from a treetop bird that I eventually identified as a Rufous-crowned Greenlet (*H. poicilotis*). I knew "this" bird well from earlier studies in woodlots to the north (Willis 1979) where it was a forest-edge and scrub bird and sang a musical "tooweedy, tooweeder . . ." complex song.

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FIG. 1. Distribution of sympatric greenlets in São Paulo State. A. Mandurí. B. Itapetininga. C. Ibití. D. Terra Preta. E. Mogi das Cruzes. F. Corumbataí. G. Fazenda Barreiro Rico. H. Descalvado. J. Fazenda Santa Genebra. K. Intervales. M. Ipanema. N. Botucatu. P. Jaguaraiva, Paraná.

Further observation confirmed that the simple song (Fig. 2A, B) involved phrases that end on a high pitch and was confined to birds with a blackish ear patch in the humid and montane south and east of São Paulo. The complex song involved alternating phrases that end low (Fig. 2C) and was confined to birds with grayish faces in the mesic interior of the state. In the Museum of Zoology of the Univ. of São Paulo (MZUSP), I found that the blackish ear patch occurred in *H. p. poicilotis* and the grayish face in *H. p. amaurocephalus.*

Morphology.—The initial look at specimens in MZUSP indicated that the two forms were rather similar, as reported by Hellmayr (1935) and Pinto (1944a). After hearing the two song types a few meters apart (below), I returned to the MZUSP collection and found that there were constant differences in color, especially head color. Color of the underparts, suggestive of intergradation, depends to some extent on how much the preparator closed the skin. Hellmayr (1935) also emphasized the larger size of southern *H. amaurocephalus* as an approach to *H. poicilotis,* but approach in size may or may not indicate hybridization.

The Rufous-crowned Greenlet has yellowish underparts, a blackish

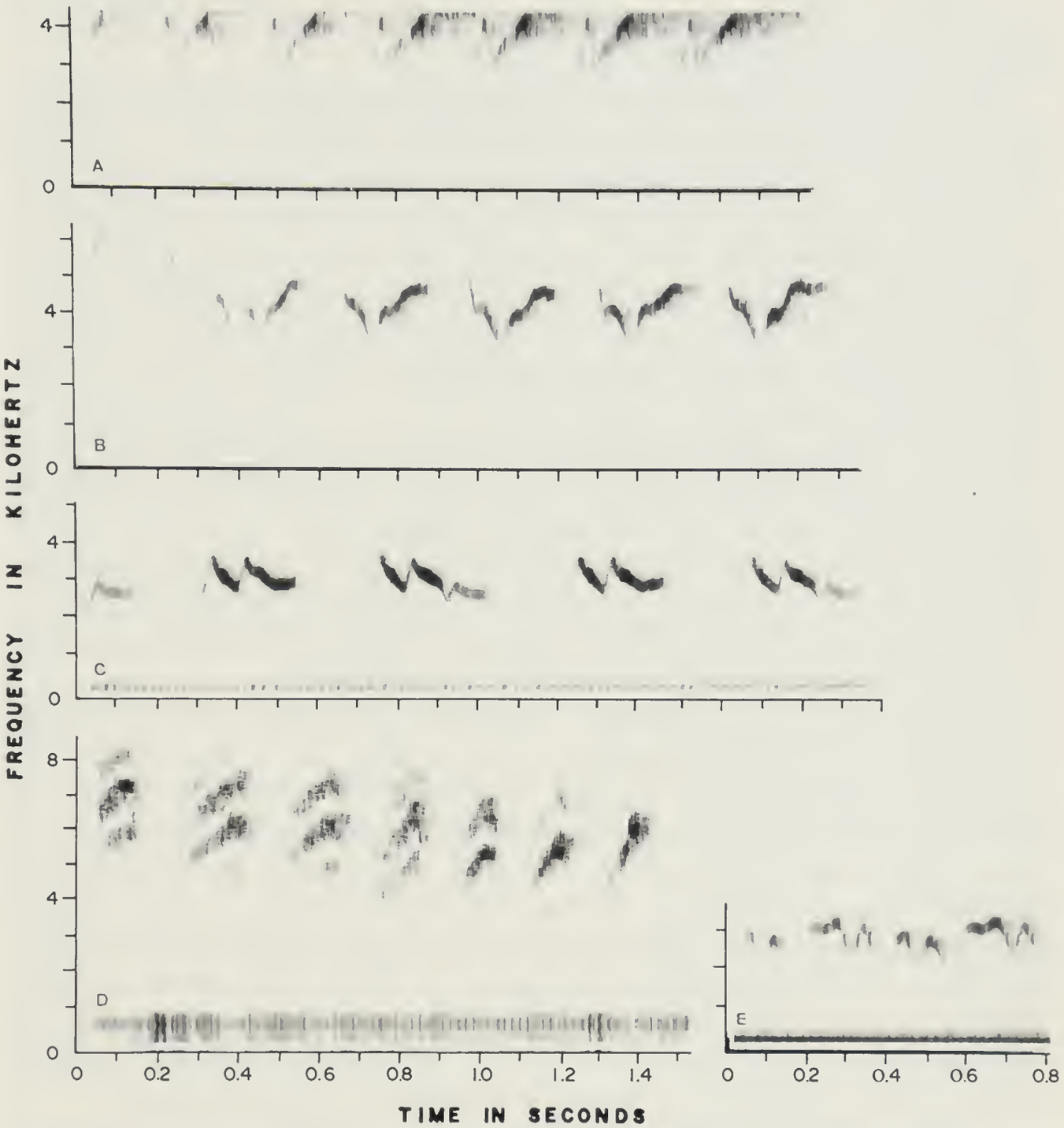

FIG. 2. Sonograms of *Hylophilus poicilotis* (A, "tweed, tweed . . ." song from Manduri; B, "tweedy, tweedy . . ." from Serra da Bocaina National Park) and *H. amaurocephalus* (Descalvado). C. "Chwee'erter . . ." song. D. "Jwai, jwai . . ." scolds. E. "Dee-terwee-ter-teebit" of presumed female.

auricular patch, and a grizzled, grayish face and forecrown. It has a short bill with dark maxilla and dark reddish-brown eyes. *Hylophilus amaurocephalus,* which may be called the Gray-eyed Greenlet, has a rufous cap extending to the bill, separated from the grayish face by a narrow but distinct pale grayish superciliary line. The auriculars are not dark, except in badly prepared specimens. The underparts are more buff than yellowish, except laterally. The bill is pale and long. The eyes are light or medium

gray. Hellmayr (1935) and other authors failed to note these differences, except for color of underparts.

Todd (1929) reported wing/tail differences denied by Hellmayr. Measurements of specimens from MZUSP do differ slightly (Table 1), notably that tail (center to tip) averages equal to the wing (chord) in *H. poicilotis* (N = 62, $t = 0.36$, ns) but almost 3 mm shorter than the wing chord in *H. amaurocephalus* ($t = 5.52$, $P < 0.01$). Since the wing and tail of *H. poicilotis* are about 55 mm and the wing/tail ratio of *H. amaurocephalus* is 56/53, the difference is not obvious; before statistical analysis, I thought Hellmayr correct. Wing and tail of small (ratio 51.6/48) *H. amaurocephalus* from northeastern Brazil also differ ($t = 4.92$, $P < 0.01$). In southeastern Brazil, its bill averages 0.2 mm higher at the front of the nostril, 0.45 mm wider at the gape angle, and 0.6–0.7 mm longer from the skull, while its tarsi are 19 and not 18 mm. Bill length, width, and tarsi of northeastern birds are about equal to *H. poicilotis,* but birds are smaller (wing, tail). Thus, relatively large bills, short tails, and long tarsi seem characteristic of *H. amaurocephalus* everywhere. Bills are significantly thick northward, especially considering the small measurements there.

Sympatry.—On 19 December 1986, at the reserve of the state Instituto Florestal at Itapetininga, southern São Paulo (Fig. 1B), I found the southern bird common in secondary gallery woodlands. A few meters away, in forest edge and bushy pastures, the complex song came from a single bird. This area had been studied for years for arboviruses by the Instituto Adolpho Lutz of São Paulo, with hundreds of captures of birds. Some specimens, mostly by Emílio Dente, eventually found their way into the collection of MZUSP in 1988. One specimen (64403), collected 2 August 1967 in the "orchard" nearby, is *H. amaurocephalus.* The rest (from the "second growth" zone) are *H. poicilotis.* Eye colors are correctly noted ("cinza claro" or light gray versus "marrom" or reddish brown).

Hellmayr (1935:159–160) found both types of greenlet (three of typical *H. poicilotis,* one of *H. amaurocephalus*) in J. Natterer's original collection of the early 1800s from Ipanema (now Varnhagen; Fig. 1M), plus one probable *H. poicilotis* that was "less yellowish" on the underparts and that he may have assumed was an intergrade. From Victoria (now Botucatu, Fig. 1N), he found one of each type. Southward, well in the range of *H. poicilotis* at Jaguaraiva, Paraná (Fig. 1P), he found one typical *H. amaurocephalus.*

Pinto (1944b) carefully studied specimens from Monte Alegre (now Ibití; Fig. 1C) without discovering that both *H. poicilotis* (Sítio Boa Vista, Fazenda Bom Jesus [mata], Fazenda Santa Izabel) and *H. amaurocephalus* (Chácara Bom Jesus, Fazenda N. Sra. Encarnação) were before him. The word "chácara" indicates a country house with a small orchard and per-

TABLE 1

MEASUREMENTS OF GREENLETS

	Wing[a]	Tail	Bill height	Bill length	Bill width	Tarsus
H. poicilotis			3.5 ± 0.22 (33)		7.7 ± 0.36 (47)	
Male	56.0 ± 2.11 (25)	55.6 ± 1.71 (25)		14.4 ± 0.51 (23)		18.2 ± 0.66 (25)
Female	53.4 ± 1.59 (26)	54.1 ± 1.91 (26)		14.0 ± 0.52 (23)		18.0 ± 0.64 (26)
H. amaurocephalus[b]			3.7 ± 0.22 (20)		8.2 ± 0.49 (20)	
Male	56.4 ± 2.11 (12)	53.7 ± 1.45 (12)		15.0 ± 0.51 (12)		19.2 ± 0.57 (12)
Female	55.3 ± 1.32 (9)	52.1 ± 1.17 (9)		14.7 ± 0.61 (9)		19.2 ± 0.61 (9)
H. amaurocephalus[c]	51.6 ± 1.38 (11)	48.0 ± 1.94 (10)	3.9 ± 0.18 (8)	14.0 ± 0.62 (12)	7.8 ± 0.35 (10)	17.7 ± 0.64 (12)

[a] $\bar{x}$ ± SD (in mm; N); nonsignificant differences between sexes shown only for bill length (*H. amaurocephalus*) and tarsi, where interspecific differences significant for males and/or females. Wing length not significant between males of the two species southward.

[b] S. Paulo, Minas Gerais.

[c] Bahia-Ceará.

haps scrub. "Mata" indicates forest, "sítio" a small farm between the size of a chácara and "fazenda" or ranch.

In MZUSP, other sympatric specimens of the two species are from Terra Preta and Mogi das Cruzes (Fig. 1D, E), so that the zone of sympatry passes across São Paulo, one of the world's largest although most deforested cities.

Habitat and habits.—H. amaurocephalus ranges from the dry woodlands of northeastern Brazil (Piauí, Paraiba) south at least to northern Paraná (Hellmayr 1935). It regularly occurs 1–10 m from the ground in scrubby, overgrown pastures and forest borders or irregular fire-burned woodlands; at times it sings in the forest canopy (observations near Murici, Alagoas), at least in regions where there are no *H. poicilotis*. The song near Murici and on the Chapada do Araripe, Ceará, is the same complex type as in São Paulo. Songs are more frequent in the morning and in the spring and summer.

It hops actively in dense foliage of branches or vines, pecking arthropods here and there; one at Corumbataí (Fig. 1F) got a spider from its web and held the prey in one foot while tearing it apart with the bill. Another bird at Fazenda Barreiro Rico, Anhembí (Fig. 1G) also held prey with the foot.

Birds normally occur in well-separated pairs, and the singing bird quickly comes to playback. The other (presumably female) then comes up and may give a special song (Fig. 2E). Both scold the observer (Fig. 2D). From 11:03 to 11:30, on 1 January 1989, in tall bush-overgrown abandoned fields near Descalvado (Fig. 1H), the presumed male sang faintly as he followed the female to and from a thin cup nest of green moss and white plant down, pendant 4.5 m in a forklet and a dense projecting tuft of leaves of a dense vine over a small tree. The male scolded, probably at me, as he hopped near the nest while the female sat and worked for long or short periods. At 11:30, a single visiting bird added a bit of down to the nest after scolds and a faint song; perhaps the male was helping. The bird(s) got material low in bushes 50–100 m away on several trips.

On 21 January 1978, a large young bird was fed out of the nest in Campinas (Faz. Santa Genebra, Fig. 1J). In the fall and winter, one often encounters groups of 3–4 birds, which are likely to be family groups. They regularly occur in mixed flocks but sometimes forage alone.

H. poicilotis ranges at least from the mountains of Espirito Santo (Santa Tereza, specimen in MZUSP; photographed in Dunning 1982) to Rio Grande do Sul and across southern São Paulo (Bauru and Porto Cabral specimens, MZUSP) to Argentina, Paraguay, and Bolivia. It occurs in the canopy and edges of humid or fairly humid forests, woodlands, and tall second growth, where it hops and pecks arthropods in fairly dense foliage. When bamboos occur next to dense dicot foliage, it hops in both, but it does not use bamboos otherwise.

Behavior and territory are much as in *H. amaurocephalus,* except that one ate some fruits of *Trema micrantha* (Melastomataceae) at Intervales (Fig. K) in March. Fruits were registered in stomachs of this or *H. amaurocephalus* by Schubart et al. (1965:222) and by Kuhlmann and Kühn 1947 (*Trichilia clausseni,* Meliaceae; specimens confirmed as *H. poicilotis* in MZUSP by collectors' numbers).

Belton (1985:166) saw one carrying green moss on 29 September 1975 in Rio Grande do Sul, suggesting that the nest may be mossy like that of *H. amaurocephalus.* A huge oven nest registered by von Ihering (1900: 205), of material of marsh plants, has almost no chance of belonging to a vireo. One often sees groups of 3–6 individuals in fall or winter, suggesting families with brood size larger than in *H. amaurocephalus.* The groups are often in mixed flocks. A faint "chek" or "chi-chek" goes between members of groups.

Discussion.—Sibling species, similar enough in morphology and behavior to confuse scientists or observers for many years, are well known. Polymorphism, in which birds of different morphology turn out to be the same species, is also rather frequent (but seems unlikely for these greenlets). Sibling and polymorphic species show that one can have significant genetic changes without morphological ones and vice versa. Although sibling species raise the specter of possible sympatric speciation, while polymorphs suggest that long geographic separation may have failed to cause speciation, one would need further evidence to prove either suggestion. Patton and Smith (1981) suggest, using electrophoresis, that geographical separation started long ago for two morphologically different pocket gopher populations that still interbreed, while rapid genetic divergence with recent geographic separation within one of the populations has produced siblings or "paraphyletic speciation." Avise et al. (1982) explained large electrophoretic differences in Vireonidae as a result of slow morphological change. One could argue that birds that depend on vocalizations to recognize their species (Tyrannidae, perhaps Vireonidae) might evolve different morphologies rather slowly, leading to sibling species. Johnson et al. (1988) suggested that overall changes in Vireonidae may occur at normal rates if they are undersplit taxonomically, perhaps due to taxonomic emphasis on plumages rather than on voice or other aspects.

The present case, in which birds considered subspecies turn out to be good species, indicates that Johnson et al. (1988) may be right about taxonomic undersplitting in vireos and that there may be other sibling species about.

It seems that sibling species can appear under the noses of active ornithologists. São Paulo is one of the most studied regions of Latin America, with large collections (see Pinto 1944a, 1978). The *Hylophilus* case here and another case in Formicariidae (Willis 1988) are surprising, consid-

ering that these birds are sympatric next to one of the largest cities in the world. Morphological differences that are obvious, once pointed out, completely escape one's attention in the field or in a museum tray. With little support for taxonomy, few persons spend much time on each study, resulting in superficial study of such birds as the greenlets. The number of cases of splitting and lumping in recent years, even in North America, suggests that birds may be well known, but not well enough. Alpha taxonomy is still needed.

Conservation.—Taxonomy has some relevance to conservation, especially when a species is split. Each form automatically gains a smaller range and a smaller world population. Few people worry about subspecies, especially in Latin America (Willis and Oniki 1982), compared to those who worry about "endangered species." When the different bird is not even recognized as a separate subspecies or population, the lack of attention is even worse (Willis 1988). Those who compose lists of "endemic" species sometimes consider world ranges in their decisions as to how many species are endemic in a certain area and hence how worthwhile a park may be in that area. If we oversplit some forms and undersplit others, we may protect the wrong areas.

In the case of the two species of *Hylophilus,* no immediate conservation problems are evident. The northern form survives in scrubby second growth. The southern one is less adaptable, more likely to lose wooded habitat, but it has a fairly wide range.

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COMPARISON OF NESTING HABITAT OF COEXISTING SHARP-SHINNED AND COOPER'S HAWKS IN MISSOURI

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ABSTRACT.—We studied the vegetative structure at nest sites of Cooper's Hawks (*Accipiter cooperii*) in two different habitats and of Sharp-shinned Hawks (*A. striatus*) in one habitat in Missouri. Sixteen Sharp-shinned Hawk nests occurred in pine (*Pinus* spp.) habitat and one in mixed pine-hardwood habitat. Thirty-three Cooper's Hawk nests occurred in pine habitat and 10 in oak-hickory (*Quercus-Carya*) hardwood habitat. Sharp-shinned Hawks nested primarily in trees with normal growth form and placed nests in the tree canopy, whereas Cooper's Hawks used mostly deformed trees and tended to place nests below the tree canopy. Vegetative structure at nest sites in pine habitat was similar for both accipiters. Cooper's Hawk nest sites in pine and hardwood habitat were similar in vertical structure but differed in horizontal structure. Vertical structure is probably a more important factor in accipiter nest-site selection than horizontal structure. *Received 15 Nov. 1990, accepted 10 June 1991.*

Quantifying the vegetative structure of nesting habitat is useful to understanding habitat selection and resource use by sympatric species. This information can be used by resource management agencies to develop strategies for enhancing habitat suitability. In Missouri, Sharp-shinned (*Accipiter striatus*) and Cooper's hawks (*A. cooperii*) have been designated as rare (Missouri Dept. of Conservation 1991). However, there has been a paucity of research directed at either species in the state and hence little is known about their habitat requirements.

Several studies have quantified and compared nest-site habitat for these accipiters in Utah (Fischer 1986), Utah-Idaho (Hennessey 1978), and Oregon (Reynolds et al. 1982, Moore and Henny 1983). Fischer (1986) concluded that each accipiter selected distinct nesting habitats. Reynolds et al. (1982) reported that these species used nest sites with different structures and that these differences were associated with stand age. Reynolds et al. (1982) also indicated that there was overlap in nesting habitat used by Sharp-shinned and Cooper's hawks as did Moore and Henny (1983).

Although nesting habitat has been described in other regions of the country, this information cannot be extrapolated to the pine and oak-hickory forests in Missouri. Therefore our objectives were to determine the vegetative structure of nest sites used by Cooper's and Sharp-shinned

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hawks and to determine if interspecific differences existed in nest sites used by these two accipiters in Missouri.

STUDY AREA AND METHODS

This study was concentrated in the Ozark and Ozark Border Natural Divisions of Missouri (Thom and Wilson 1980). Most of the forest cover of Missouri occurs in these divisions (Spencer and Essex 1976). Oak-hickory is the major forest type of the divisions, although shortleaf pine (*P. echinata*), shortleaf pine-oak-hickory, and bottomland hardwood types are also prominent. Oak-hickory hardwoods comprise about 77% of the forest cover of the state, shortleaf pine about 1%, and shortleaf pine-oak-hickory about 2% (Spencer and Essex 1976).

Data collection.—Two approaches were used to locate accipiter nests in 1985 and 1986. We solicited information regarding the nesting activity of accipiters through mail surveys and notices published in conservation newsletters (Kritz 1989). We also searched forest tracts. Our survey was sent statewide to about 400 wildlife biologists and managers, foresters, conservation agents, park naturalists, falconers, and birdwatchers. The first survey was sent prior to the start of the 1985 breeding season to solicit information about historic nest locations. Surveys also were sent at the end of the 1985 and 1986 breeding seasons.

We systematically searched tracts of forest cover that in most instances corresponded to a forest stand. Because we wanted to locate the maximum number of nests, searches were concentrated in stands we believed provided suitable nesting habitat. Thus, most searches were conducted in pine habitat because nests in Missouri have been found primarily in pine habitat. This resulted in a disproportionate number of searches in pine habitat.

Before each search, territorial calls of Sharp-shinned and/or Cooper's hawks or Great Horned Owls (*Bubo virginianus*) were broadcast using a cassette tape player (Fuller and Mosher 1981, Rosenfield et al. 1985). If accipiters responded to the tape, the vocalizations and/or flights were followed directly to their origin, which was usually near the nest. If there was no response to the calls, the tract was still searched until either a nest was found or the tract was searched completely. We used a similar procedure in 1986 for rechecking all nest sites located during 1985 except taped calls were broadcast starting at the 1985 nest tree, and all forest habitat within a 300 m radius of the nest tree was searched.

We conducted nest-site habitat evaluation after young had fledged. A nest site was defined as the nest tree and a 0.04-ha circular plot centered on it (Titus and Mosher 1981). Habitat evaluation procedures followed James and Shugart (1970) and Titus and Mosher (1981) (Table 1). Variables measured at nest sites and associated with overstory coverage, understory coverage, ground coverage, and canopy height were collectively used to characterize the vertical vegetative structure at nest sites (Table 1). Variables associated with stem densities, stem diameters, and basal areas were used to characterize the horizontal vegetative structure at nest sites.

Statistical analysis.—Nests were grouped according to the habitat where they occurred. The habitat categories were pine (>50% of the overstory trees were pine), hardwood (>50% of the overstory trees were oak and hickory), and mixed pine-hardwood (>25% of the overstory trees were pine and oak-hickory but neither category alone made up >50%). Only one nest (Sharp-shinned Hawk) was found in the pine-hardwood habitat, and data for this nest were not included in the analysis.

Chi-square analysis (Snedecor and Cochran 1980) was used to test for intra- and interspecific differences in the frequency nests occurred in trees having different growth forms (normal or deformed) and nest placement relative to the canopy (below or within). Nest trees with normal growth form had one main bole and normal branching patterns. Trees

Table 1

Description and Measurement Procedure for Habitat Variables Used to Characterize Nest Sites of Sharp-shinned and Cooper's hawks in Missouri, 1985–1986

Variable	Description and procedure
Coniferous canopy	Percent of coniferous canopy cover[a]
Deciduous canopy	Percent of deciduous canopy cover[a]
Total canopy	Percent total canopy cover[a]
Coniferous understory	Percent of coniferous understory cover[a]
Deciduous understory	Percent of deciduous understory cover[a]
Total understory	Percent total understory cover[a]
Total ground cover	Percent total ground cover[a]
Canopy height	The mean of five measures (m) taken to the top of the canopy (measured with clinometer)
Small shrubs	Number of small (≤2.5 cm dbh and 0.5–1.4-m height) shrubs per ha[b]
Large shrubs	Number of large (≤7.6 cm dbh and ≥1.5-m height) shrubs per ha[b]
Understory trees	Number of understory trees >9 cm dbh per ha[c]
Overstory trees	Number of overstory trees per ha[c]
Total trees	Number of over and understory trees per ha[c]
Overstory trees <25	Number of overstory trees <25 cm dbh per ha[c]
Overstory trees 25–50	Number of overstory trees 25–50 cm dbh per ha[c]
Overstory trees >50	Number of overstory trees >50 cm dbh per ha[c]
DBH	Average diameter (cm) of all overstory trees in 0.04 ha plot (diameter tape)
Basal area	Basal area (m^2/ha) (taken at center of 0.04 ha plot with 10 BAF prism)
Age	Age of stand nest site was in (estimated by increment boring of ≥ two dominant trees)
Stand size	Size (ha) of stand nest site was in (taken from aerial photos)
Slope	Percent slope for nest site (measured with clinometer)
Elevation	Elevation (m) of the nest site (taken from USGS 7.5 min. topographic maps)

[a] Percentages based on 10 ocular tube readings each along four 11.3-m transects that intersected at the nest tree. Overstory trees had the majority of their foliage in the forest canopy layer, and understory trees had the majority of their foliage below the forest canopy layer.

[b] Extrapolated to per ha basis from measurements within four 11.3 × 1.8-m strip transects that intersected at the nest tree.

[c] Extrapolated to per ha basis from counts in 0.04-ha plot.

with deformed growth form had either a main bole that split into ≥ two large forks and/or an abnormal whorl of branches near the top. At four sites, we could not determine growth form and/or nest placement because of logging (N = 1) or because nests fell out of nest trees before we evaluated habitat (N = 3).

We analyzed quantitative nest-site data using SAS programs (SAS Institute 1985). Distributions of nest-site variables were tested for normality using Shapiro-Wilk tests, and

variance was tested using *F*-tests. Most variables had distributions that were not normal and/or variance was heterogeneous. Transformations were ineffective in normalizing distributions or stabilizing variance. Therefore, Mann-Whitney tests were used to determine if there were differences in habitat variables between Cooper's and Sharp-shinned hawk nest sites in pine habitat and between Cooper's Hawk nest sites in pine and hardwood habitat. Because of the numerous (N = 51) comparisons made, and to minimize the chance for a Type I error, we used α/N (0.05/51) = 0.001 as the significance level in all analyses.

RESULTS

We conducted searches in 394 forest tracts. Fifty-one percent of the searches were in shortleaf pine stands, 23% were in stands of oak-hickory hardwoods, 17% were in stands of shortleaf pine mixed with exotic pines (shortleaf is the only pine species native to Missouri) or exotic pines without shortleaf, and 9% were in stands of mixed pine-hardwoods or other coniferous and hardwood types.

Fifty-two (87%) nests were found through tract searches and eight (13%) were found by cooperators. Overall, 43 Cooper's Hawk and 17 Sharp-shinned Hawk nests were located. The total of 60 nests represents 46 distinct accipiter nesting territories when considering reoccupancy of 1985 sites in 1986. Of these, 31 were Cooper's Hawk and 13 were Sharp-shinned Hawk nesting territories. Two nesting territories were used by both species, but they used them in alternate years. A nesting territory is an area containing one or more nests within the range of one mated pair of birds (Steenhof 1987).

Sharp-shinned Hawk.—Sixteen nests occurred in pine habitat; 15 were in shortleaf pine stands, and one was in a mixed species pine stand. One nest was in shortleaf pine-oak habitat. All of the pine stands used, except two, were planted pine plantations. Pine sites were medium-aged (range 25–49 years) with high tree density and basal area and high percent canopy coverage (Table 2). Most overstory trees were <25 cm dbh, and the mean diameter for overstory trees was 20.8 cm (Table 2).

All nests were found in shortleaf pine trees except one that was in a Virginia pine (*P. virginiana*). Ten of 15 (67%) nest trees had normal growth form but the difference in the number of normal and deformed trees used was not significant ($\chi^2 = 1.7$, df = 1, $P > 0.001$). More nests (80%, 12 of 15) were located in the live canopy than below the canopy, but the difference was not significant ($\chi^2 = 5.4$, df = 1, $P > 0.001$).

Cooper's Hawk.—Thirty-three nests occurred in pine habitat; 17 were in shortleaf pine stands, 15 were in mixed species pine stands, and one was in a scotch pine (*P. sylvestris*) stand. Ten nests occurred in hardwood habitat. All of the pine stands used except one were pine plantations. Pine nest sites were medium-aged (range 25–49 years) and dense with high percent canopy coverage, tree density, and basal area (Table 2). Most

TABLE 2

COMPARISONS OF MEAN VALUES FOR HABITAT VARIABLES MEASURED AT SHARP-SHINNED AND COOPER'S HAWK NEST SITES IN MISSOURI, 1985–1986

Variable	Pine habitat		Hardwood habitat
	Sharp-shinned	Cooper's	Cooper's
Coniferous canopy (%)	78.0 ± 2.9[a] (14)	75.7 ± 2.8 (31)	0.0 ± 0.0 (9)
Deciduous canopy (%)	4.3 ± 2.5 (14)	5.2 ± 1.2 (31)	82.5 ± 3.2[c] (9)
Total canopy (%)	82.3 ± 1.7 (14)	80.9 ± 2.1 (31)	82.5 ± 3.2 (9)
Coniferous understory (%)	9.4 ± 3.1 (11)	5.2 ± 1.1 (29)	0.5 ± 0.5 (9)
Deciduous understory (%)	37.4 ± 7.0 (11)	38.9 ± 4.7 (29)	56.0 ± 5.1 (9)
Total understory (%)	46.8 ± 7.8 (11)	44.1 ± 4.6 (29)	56.5 ± 5.2 (9)
Total ground cover (%)	35.5 ± 4.0 (12)	41.1 ± 3.9 (29)	34.2 ± 5.9 (9)
Canopy height (m)	16.7 ± 0.6 (15)	18.4 ± 0.4 (33)	20.0 ± 0.8 (10)
Small shrubs (No./ha)	6617 ± 1340 (15)	8176 ± 953 (32)	4650 ± 1484 (10)
Large shrubs (No./ha)	4467 ± 553 (15)	4733 ± 595 (32)	2863 ± 837 (10)
Understory trees (No./ha)	382 ± 55 (15)	300 ± 34 (33)	320 ± 44 (10)
Overstory trees (No./ha)	988 ± 113 (15)	838 ± 65 (33)	243 ± 31[c] (10)
Total trees (No./ha)	1370 ± 132 (15)	1138 ± 79 (33)	563 ± 44[c] (10)
Over. trees <25 (No./ha)	857 ± 140 (15)	685 ± 78 (33)	123 ± 32[c] (10)
Over. trees 25–50 (No./ha)	131 ± 35 (15)	153 ± 23 (33)	113 ± 20 (10)
Over. trees >50 (No./ha)	0 ± 0 (15)	0 ± 0 (33)	7 ± 5 (10)
DBH (cm)	20.8 ± 0.9 (15)	21.8 ± 0.6 (33)	30.8 ± 2.2[c] (9)
Basal area (m^2/ha)	37.2 ± 2.0 (15)	36.8 ± 1.5 (32)	17.8 ± 2.3[c] (10)
Age (years)	32.7 ± 1.9 (15)	32.0 ± 1.1 (33)	87.1 ± 12.2[c] (10)
Size (ha)	11.8 ± 4.7 (16)	4.1 ± 0.7 (33)	52.6 ± 12.8[c] (10)

TABLE 2
CONTINUED

Variable	Pine habitat		Hardwood habitat
	Sharp-shinned	Cooper's	Cooper's
Slope (%)	5.1 ± 1.1 (16)	10.0 ± 1.7 (33)	16.1 ± 3.7 (10)
Elevation (m)	308 ± 17 (16)	263 ± 11 (33)	263 ± 20 (10)

[a] All values are means ± SE; sample size is in parentheses and varies due to logging or late sampling.
[b] Indicates significant difference ($\alpha = 0.05/51 = 0.001$ significance level) for Sharp-shinned Hawk vs Cooper's Hawk in pine habitat.
[c] Indicates significant difference ($\alpha = 0.05/51 = 0.001$ significance level) for Cooper's Hawk in pine vs oak-hickory habitat.

overstory stems were <25 cm dbh, and the mean diameter for overstory trees was 21.8 cm (Table 2).

Nests sites in hardwood habitat were in moderately dense stands with a mean age of 87.1 years (range 34–154 years) and high percent canopy coverage (Table 2). The proportions of overstory trees <25 cm dbh and those 25–50 cm dbh were similar, and the mean diameter for overstory trees was 30.8 cm (Table 2).

In the pine habitat, 22 nests were located in shortleaf pine trees, six were in scotch pine trees, two were in eastern white pine (*P. strobus*) trees, two were in jack pine (*P. banksiana*) trees, and one was in an eastern red cedar (*Juniperus virginiana*) tree. In the hardwood habitat, northern white oak (*Q. alba*) was used most often (60%, 6/10) as the nest tree; whereas, black oak (*Q. velutina*), southern red oak (*Q. falcata*), northern red oak (*Q. rubra*), and blackjack oak (*Q. marilandica*) were each used once.

Intraspecific comparisons (Cooper's Hawk).—Horizontal structure of nest sites differed between habitats. Nest sites in pine habitat had significantly more overstory trees ($P = 0.0001$) of smaller average diameter ($P = 0.0001$), more total trees ($P = 0.0001$), more trees <25 cm dbh ($P = 0.0001$), and greater basal area ($P = 0.0001$) than sites in hardwood habitat (Table 2). On the other hand, there were no differences ($P > 0.001$) in vertical structure between pine and hardwood sites as measured by overstory and understory canopy cover (total), total ground cover, and canopy height. Nest sites in pine habitat occurred in younger ($P = 0.0001$) and smaller ($P = 0.0001$) stands than in hardwood habitat (Table 2).

Including both pine and hardwood habitats, 28 of 43 nest trees used by Cooper's Hawks were deformed, but the difference in the proportion

of normal (35%) and deformed (65%) trees used was not significant ($\chi^2 = 3.9$, df = 1, $P > 0.001$). Twenty-two of 40 nests were located below the live canopy. However, the proportion below the canopy (55%) and in the canopy (45%) was not significantly different ($\chi^2 = 0.4$, df = 1, $P > 0.001$). A higher percentage of coniferous than deciduous nest trees were deformed (73% vs 40%), but the difference was not significant ($\chi^2 = 3.6$, df = 1, $P > 0.001$).

Interspecific comparisons (pine habitat).—Habitat variables at nest sites associated with topography, stand age, and either horizontal or vertical structure did not differ between accipiters ($P > 0.001$) (Table 2). However, Sharp-shinned Hawks nested primarily on ridgetops (69%, 11/16), whereas Cooper's Hawks tended to nest along ridge slopes (52%, 17/33).

Most (73%, 24/33) Cooper's Hawk nest trees were deformed and most (67%, 10/15) Sharp-shinned Hawk nest trees were normal but interspecific difference in the growth form of the nest tree was not significant ($\chi^2 = 6.8$, df = 1, $P > 0.001$). Most (80%, 12/15) Sharp-shinned Hawk nests were within the live canopy of the nest tree whereas Cooper's Hawk nests tended to be below the canopy (60%, 18/30), but nest placement relative to tree canopy was not significantly different between accipiters ($\chi^2 = 6.2$, df =1, $P > 0.001$).

DISCUSSION

Sharp-shinned and Cooper's hawks both used dense stands of pine of similar age for nesting. The vegetative structure of nest sites overlapped greatly between species. Accipiter use of dense forest stands in this study agrees with results from other comparative studies (Hennessey 1978, Reynolds et al. 1982, Moore and Henny 1983, and Fischer 1986). The interspecific overlap in nest-site habitat also was consistent with other studies (Reynolds et al. 1982, Moore and Henny 1983) although the degree of overlap in our study was much greater. In contrast, Fischer (1986) reported that these species used distinct habitats.

Reynolds et al. (1982) and Moore and Henny (1983) reported that differences in nest-site habitat selection between accipiters were associated with forest successional development and that Sharp-shinned Hawks used younger stands of earlier successional development than Cooper's Hawks. Fischer (1986) noted that interspecific differences in nesting habitat did not correspond directly with successional development but that the structure of his nest sites differed in the same way as in the other studies. However, we were unable to detect any clear pattern in habitat selection between accipiters associated with forest successional development.

We were unable to detect differences in the vegetative structure at nest sites in pine habitat between accipiters. Also, we were unable to detect

significant differences between accipiters in the type of nest trees used and the placement of nests within the nest tree. However, we did observe a strong tendency for Sharp-shinned Hawks to use trees with normal growth form and to place nests in the nest tree canopy. On the other hand, Cooper's Hawks tended to use trees with deformed growth form and tended to nest below the canopy. Although these differences were not significantly different at the adjusted $\alpha = 0.001$ level, they were significant at the $\alpha = 0.05$ level.

Differences in the type of nest tree used and placement of nest within the nest tree may be the result of differences in accipiter body size (Moore and Henny 1983, Fischer 1986). The smaller Sharp-shinned Hawk may nest in the canopy more often because it can fly in and out of dense canopies more easily than the larger Cooper's Hawk. Most (79%, 19/24) deformed trees used by Cooper's Hawks had top deformities and the branch whorls associated with these deformities generally provided more support than branches extending from boles of trees with normal growth form. Also top deformities usually occurred below the nest tree canopy. Thus Cooper's Hawks may use deformed trees more often because they build larger nests than Sharp-shinned Hawks that require more support and their nests would tend to be below the canopy. We did not determine the availability of deformed trees, but in all cases most trees at the nest sites had normal growth form.

Interspecific differences in predation pressure (Moore and Henny 1983, Fischer 1986) also may explain differences in nest placement. In our study, nests placed in the canopy appeared to be more concealed that those below the canopy because live branches were present both above and below them. Smaller raptors experience greater predation pressure than larger raptors (Newton 1979), and Cooper's Hawks will prey upon Sharp-shinned Hawks (Jones 1979).

Vertical structure was similar in the pine and hardwood habitats used by Cooper's Hawks, whereas horizontal structure differed. Fewer hardwood tree stems, of larger mean diameter, were required to provide the same vertical structure provided by pine habitat. However, the trees were much older in hardwood habitat than in pine habitat. Thus, it generally takes longer to develop this vertical structure in hardwood habitat. Because vertical structure was similar in both habitat types it is probably a more important factor, at least on a gross level, than horizontal structure in nest-site selection.

The vegetative structure of Cooper's Hawk nest sites in pine habitat in this study was similar to that reported by Reynolds et al. (1982) and Moore and Henny (1983). Nest sites in hardwood habitat (Hennessey 1978, Titus and Mosher 1981) were similar to our hardwood sites. Al-

though nests in hardwood habitat occurred in stands that were larger in size than in pine habitat, hardwood stands in Missouri are generally larger than pine stands, and this likely explains the difference.

Although we did not find Sharp-shinned Hawk nests in hardwood forest, we do not believe this species avoids this habitat in Missouri. The Sharp-shinned Hawk nests in hardwood habitats in other parts of its range (Hennessey 1978, Reynolds et al. 1982, and Fischer 1986), and it is likely it uses this habitat in Missouri. Our inability to find nests in hardwood habitat may be more a reflection of the scarcity of this species in Missouri and/or our concentrating search efforts in pine habitat.

ACKNOWLEDGMENTS

This study was funded by the Natural History Section of the Missouri Dept. of Conservation, the Missouri Agricultural Experiment Station, the Missouri Cooperative Fish and Wildlife Research Unit, and the E. Sydney Stephens Fellowship Fund. J. Wilson was especially helpful during all stages of the project. The biologists, foresters, and managers of the Missouri Dept. of Natural Resources, Dept. of Conservation, and the U.S. Forest Service-Mark Twain National Forest provided invaluable assistance in locating and monitoring nests and provided maps and forest inventory data. We also thank the many falconers, birdwatchers, and outdoor enthusiasts who provided helpful information. We thank R. Renken for helpful comments on earlier drafts of this manuscript. This is manuscript number 11,440 of the Missouri Agricultural Experiment Station.

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WILSON ORNITHOLOGICAL SOCIETY MEETINGS—1992

The Wilson Ornithological Society will meet with the Florida Ornithological Society at the Hilton Inn Gateway, U.S. Highway 192, Kissimmee, Florida, 9–12 April 1992. Sponsoring organizations are Archbold Biological Station, Florida Audubon Society, Kissimmee Valley Audubon Society, Lake Region Audubon Society, Orange Audubon Society, and Sea World. HERBERT W. KALE II, Florida Audubon Society, 460 Highway 436, Suite 200, Casselberry, FL 32707 (407-260-8300, FAX 260-9652) will chair the Local Committee. KEITH L. BILDSTEIN, Dept. of Biology, Winthrop College, Rock Hill, SC 29733 (803-323-2111, FAX 323-2347) will chair the Scientific Program Committee. Deadline for submittal of abstracts is 1 February 1992. The Circular of Information was mailed to WOS and FOS members in early December. Others should write to Dr. Kale for a copy. Students desiring to share room costs with other students at the Hilton should contact Dr. Kale for assistance no later than February 1 and prior to sending reservations to the hotel. The meeting will include a reception at Sea World, an art exhibit by Florida bird artists, and field trips to see Florida specialties. Walt Disney World, EPCOT, MGM Studios, Universal Studios, Sea World, Cypress Gardens, and many other attractions are in the immediate vicinity. This will be a good meeting to bring spouses and family.

Wilson Bull., 103(4), 1991, pp. 578–597

TIME BUDGETS AND THE ADAPTIVENESS OF POLYANDRY IN NORTHERN JACANAS

Burr J. Betts[1] and Donald A. Jenni[2]

Abstract.—Time budgets of polyandrous Northern Jacanas (*Jacana spinosa*) were studied at a 2.8-ha pond in Costa Rica from Jan.–Dec. 1974. Time budgets differed significantly depending on reproductive condition, sex, location, and time of day. Although similar prior to egg laying, male and female time budgets diverged greatly when eggs or chicks were present. At that time, males reduced foraging, other somatic behaviors, and time spent off-the-pond as they assumed major responsibility for parental care, which consumed much of the early morning and late afternoon. Females, which were never seen incubating and were rarely seen brooding, maintained a high proportion of time spent foraging throughout the day and year. Females spent more time in territories where chicks were present, resulting in increased interspecific aggression, resting, and walking as they provided direct and potential predator protection. After egg laying, females reduced time spent foraging and increased time spent resting. Females helped males by brooding and accompanying chicks at times when food availability was apparently low. Females did not reduce their total foraging time in territories containing chicks. These data best support the replacement clutch hypothesis and support neither the female energetic stress nor the uniparental care hypotheses for the adaptiveness of classical polyandry in the Northern Jacana. Insufficient data exist to conclude whether a single explanation for the evolution of classical polyandry is possible for all species exhibiting some form of this mating system. *Received 4 Feb. 1991, accepted 10 April 1991.*

Avian polyandry takes two basic forms (Oring 1986). In classical polyandry, females engage in separate reproductive efforts with each of several males. In cooperative polyandry, several males share in a single reproductive effort by a female. Although cooperative polyandry is an important form of this mating system, only classical polyandry is considered in the present paper, and all further references to polyandry should be regarded as referring only to classical polyandry.

Classical polyandry is known to be the predominant mating system in only two avian species: the Spotted Sandpiper (*Actitis macularia*) (Hays 1972, Oring and Knudson 1972) and the Northern Jacana (*Jacana spinosa*) (Jenni and Collier 1972). Polyandrous mating relationships also occur infrequently in several other shorebirds that are basically monogamous (for reviews see Jenni 1974, Emlen and Oring 1977, Erckmann 1983, Lenington 1984, Oring 1986, Colwell and Oring 1988).

Hypotheses for the adaptiveness of classical polyandry can be grouped into three ecological arguments. Female energetic stress hypotheses sug-

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gest that limited food and laying-induced energy depletion of females interact to favor paternal care of the young. Food scarcity might preclude any sharing of incubation by the female (Graul et al. 1977, Lenington 1980, 1984), or it might only make it less possible for the female than for the male to do all parental care (Maynard Smith 1977, Ashkenazie and Safriel 1979, Erckmann 1981). If food supplies fluctuate, periods of scarcity would favor desertion by the female, and temporary, infrequent periods of superabundance would allow multiple clutching by the female for the same or a different male (Graul 1973, 1976; Lenington 1984).

Uniparental care hypotheses assert only that sometimes uniparental care can be more successful than biparental care but do not argue for one type of polygamy over another (Pitelka et al. 1974). Uniparental care might be more successful if frequent trade-offs at the nest increased nest predation or if there were significant competition for food between parents or between parents and offspring. The increase in reproductive fitness realized through the anti-predator or feeding benefits gained by desertion of one parent would have to be greater than any decrease in fitness resulting from uniparental care.

The replacement clutch hypothesis argues that excessive clutch loss makes polyandry adaptive for both sexes if the female, freed from parental duties, can forage more and rapidly provide replacement clutches (Jenni 1974, Emlen and Oring 1977). The male and the female would both benefit by another chance at reproduction, and in addition, the female could produce clutches for additional males.

A major problem associated with testing these hypotheses is the difficulty in measuring parental investment, particularly in terms of the cost to the parent's ability to invest in other offspring (Trivers 1972). Although relative energetic investments in the gametes can be compared, the amount of time and energy invested in all aspects of reproduction need to be analyzed (Brunton 1988). However, only a few such studies have been done on shorebirds. Time and/or energy budget data for breeding individuals of non-polyandrous species are reported by Gibson (1971, 1978), Ashkenazie and Safriel (1979), Lenington (1980), Burger (1981), Brunton (1988), and Purdy and Miller (1988). Similar studies of polyandrous species include only those by Maxson and Oring (1980) on a population of Spotted Sandpipers and Osbourne and Bourne (1977) on one pair of Wattled Jacanas (*Jacana jacana*).

Of the polyandrous shorebirds, only the tropical jacanas typically exhibit simultaneous polyandry. Female Spotted Sandpipers occasionally pair with more than one male simultaneously (Oring and Maxson 1978), but sequential pairing is much more common (Hays 1972, Oring and Knudson 1972). The best known jacana is the Northern Jacana; a detailed

description of polyandry in this species is given by Jenni and Collier (1972) and Jenni and Betts (1978). Males maintain individual territories. Breeding females are 75% larger than males and defend territories encompassing those of 1–4 males. Sex role reversal is nearly complete, with males assuming most of the nest building and parental care. Females maintain pair bonds with each male, copulating frequently with each, laying eggs for some, helping defend male territories, and providing predator protection for eggs and chicks.

In this paper we describe time budgets of a polyandrous population of Northern Jacanas. The paternal care system causes gross differences in the reproductive time budgets of the two sexes, parts of which we have reported previously (Jenni and Betts 1978). Here, we are also interested in adjustments of time allocation related to differences in location and time of day. We show how these time budgets relate to a polyandrous system and we use the time budget data to help evaluate how hypotheses of the adaptiveness of polyandry apply to this species.

METHODS

The study area, described in detail by Jenni and Collier (1972), was a shallow 2.8-ha pond at 600 m elevation near Turrialba, Costa Rica. The pond was bordered by lawn and patches of trees. Parts of the edge were overgrown by heavy stands of papyrus (*Cyperus papyrus*), but the majority of the pond was covered by water lilies (*Nymphaea ampla*) and other low vegetation which allowed observation of the birds.

Time budget data were gathered Jan.–Dec. 1974. Boundaries of the six male territories remained stable throughout this period even though one male was replaced. Early in the year two boundary changes occurred among the females as territory ownership shifted from one monandrous, one biandrous, and one triandrous female to two triandrous females. In the remaining nine months, one of these triandrous females was replaced once, but the territory boundaries remained stable. Although this population was small, we believe its social system is typical for Northern Jacanas at other permanent ponds or lakes. This population was studied from 1963 to 1976, and considerable turnover in individual birds occurred with no change in the general social structure. Also, both of us observed other, larger populations where we noticed no major differences in behavior.

We made observations through binoculars and spotting scopes from various locations around the pond. The birds were habituated to observers which made blinds unnecessary. All individuals were marked with colored leg bands. Sex was determined from size (Jenni 1974) and observations of copulation and egg laying.

We gathered instantaneous time budget data (Altmann 1974) on territory holders during all phases of their reproductive cycle. Birds were chosen for observation on the basis of reproductive condition in order to maximize sample size. Individuals in reproductive conditions under-represented in the data were chosen preferentially over others. Two to three birds could be observed at once. Data were collected at two-min intervals in two-h time blocks. An individual "data-day" consisted of observations made on one–three consecutive calendar days. When observations extended more than one day, the two-h time blocks were distributed such that all daylight hours were sampled. Day length varied from about 11.5

to 12.5 h. Observations were spread evenly throughout the year. We accumulated 86 data-days (31,428 observations) on the seven males and 42 data-days (15,633 observations) on the five females that held territories at some time during 1974. Proportions of instantaneous observations are estimates of the percentage of daylight hours spent in particular behavioral categories and are reported here as percentages of observation time.

For each instantaneous sampling point we recorded the location and behavior of the bird, or if it was out of sight, a subjective analysis of weather conditions and any other observations worth noting. For analysis, behaviors were combined into the following 12 categories which are comparable with those used by Maxson and Oring (1980) for the Spotted Sandpiper and by Brunton (1988) for the Killdeer (*Charadrius vociferus*). For some analyses, categories were further grouped as somatic, mating, and parental behaviors, following Brunton (1988).

Somatic behaviors include: (1) foraging—walking or standing with bill lowered and frequently pecking at food or poking or peering at vegetation; (2) preening—grooming feathers, bathing, scratching, or stretching; (3) resting—sitting or standing; (4) flying—normal horizontal flight; and (5) walking—walking with bill horizontal, without pecking at food or peering at vegetation and not in company of chicks.

Mating behaviors include: (1) nest building—pulling at vegetation, picking up and throwing rearward bits of vegetation, push-stepping on the nest platform, or poking bill into nest site; (2) presenting-mounting—precopulatory displaying by either sex and unsuccessful mountings; (3) copulating—mountings in which successful cloacal contact is apparently established; and (4) intraspecific aggression—aggressive and appeasement interactions involving other jacanas, most often associated with territorial defense.

Parental behaviors include: (1) incubating—sitting on the nest when eggs are present, (2) walking-with-chicks—accompanying the chicks as the latter feed, (3) brooding—sheltering one or more chicks with the body or wings, and (4) interspecific aggression—aggressive interactions involving potential predators.

Data for males were grouped into four reproductive conditions: (1) precopulation (16 days, 5726 observations)—male had neither eggs nor chicks less than 10 weeks old and was not copulating with his mate; (2) copulation (29 days, 10,686 observations)—male had neither eggs nor chicks less than 10 weeks old and was copulating with his mate; (3) incubation (16 days, 5911 observations)—male had eggs; and (4) brooding (25 days, 9105 observations)—male had chicks less than 10 weeks old. Data for females were grouped into five categories: (1) precopulation (4 days, 1431 observations)—female was not copulating with any of her males and had no mates with eggs or chicks; (2) copulation (19 days, 7087 observations)—female was copulating with one or more males and had no mates with eggs or chicks; (3) with-eggs-only (seven days, 2568 observations)—female had at least one incubating mate and may or may not have been copulating with her other males; (4) with-chicks-only (7 days, 2507 observations)—female had at least one brooding mate and may or may not have been copulating with her other males; and (5) with-eggs-and-chicks (five days, 1822 observations)—female had at least one incubating and one brooding mate and may or may not have been copulating with her third male.

Data were grouped into six time periods: dawn–08:00, 08:00–10:00, 10:00–12:00, 12:00–14:00, 14:00–16:00, and 16:00–dusk, CST. The length of the first and last periods varied due to seasonal changes in dawn and dusk times, but averaged about two hours each. Because data are reported as percentages of observation time, this variation is probably unimportant.

Time budget data were analyzed for variation related to reproductive condition, sex, location, and time of day. Nonparametric statistics were used to test for significance to avoid assuming that data were normally distributed with equal variances. Except where noted, either the Kruskal-Wallis one-way ANOVA or the Mann-Whitney *U*-test were used (Siegel 1956). Sample size is the number of data-days analyzed.

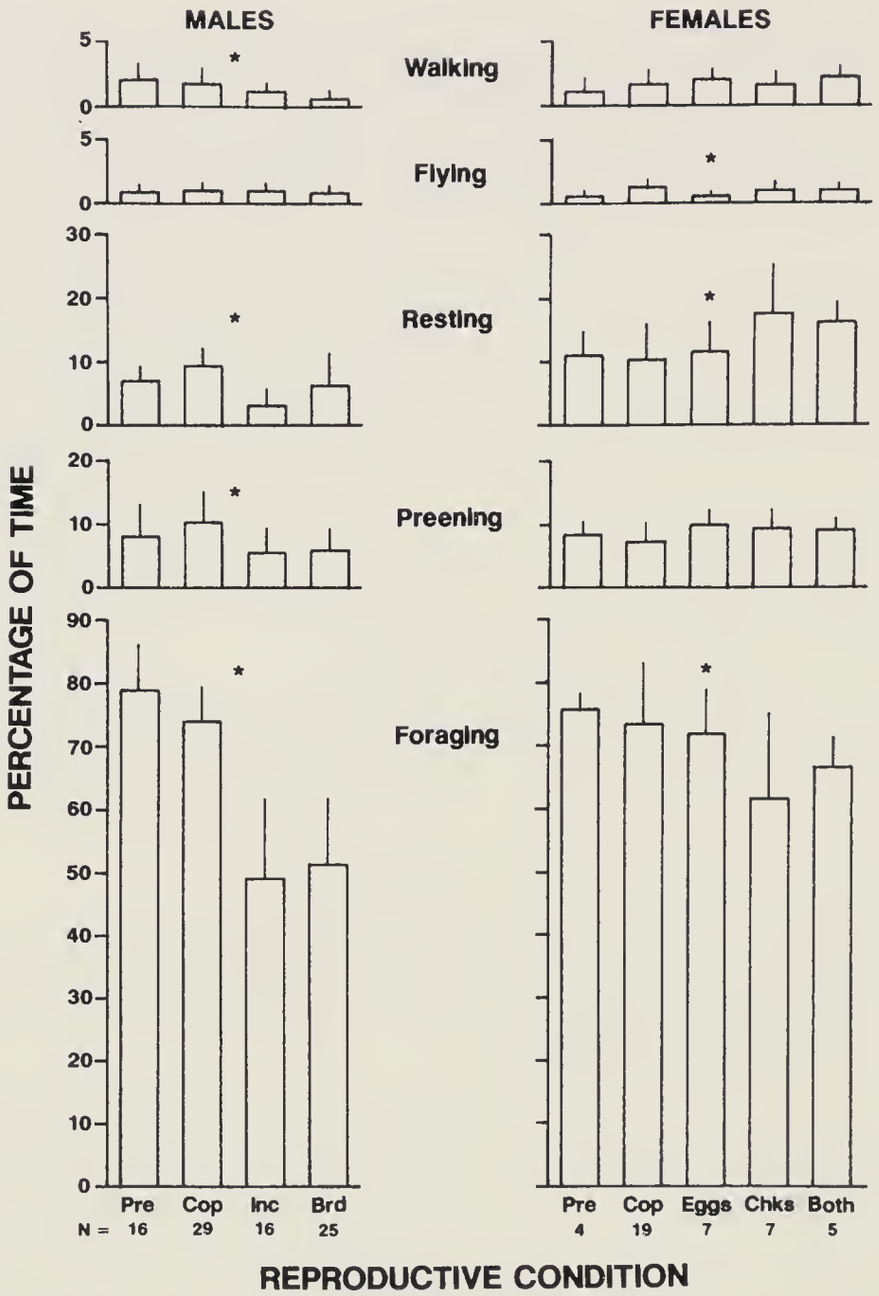

FIG. 1. Percentage of time males and females spent performing somatic behaviors as a function of reproductive condition. Pre = precopulation period, Cop = copulation period, Inc = incubation period, Brd = brooding period, Eggs = with-eggs-only period, Chks = with-chicks-only period, Both = with-eggs-and-chicks period. Statistical significance: * = $P \leq 0.05$ that there was no difference between reproductive conditions in the percentage of time spent in that behavioral category.

RESULTS

The polyandrous relationships of females and the monogynous relationships of males resulted in different reproductive cycles for the two sexes. The situation was especially complex for females whose mates could all be in different reproductive conditions. The pervasive differences between the sexes make it necessary to discuss male and female time budgets separately.

Reproductive condition differences.—The amount of time spent in most

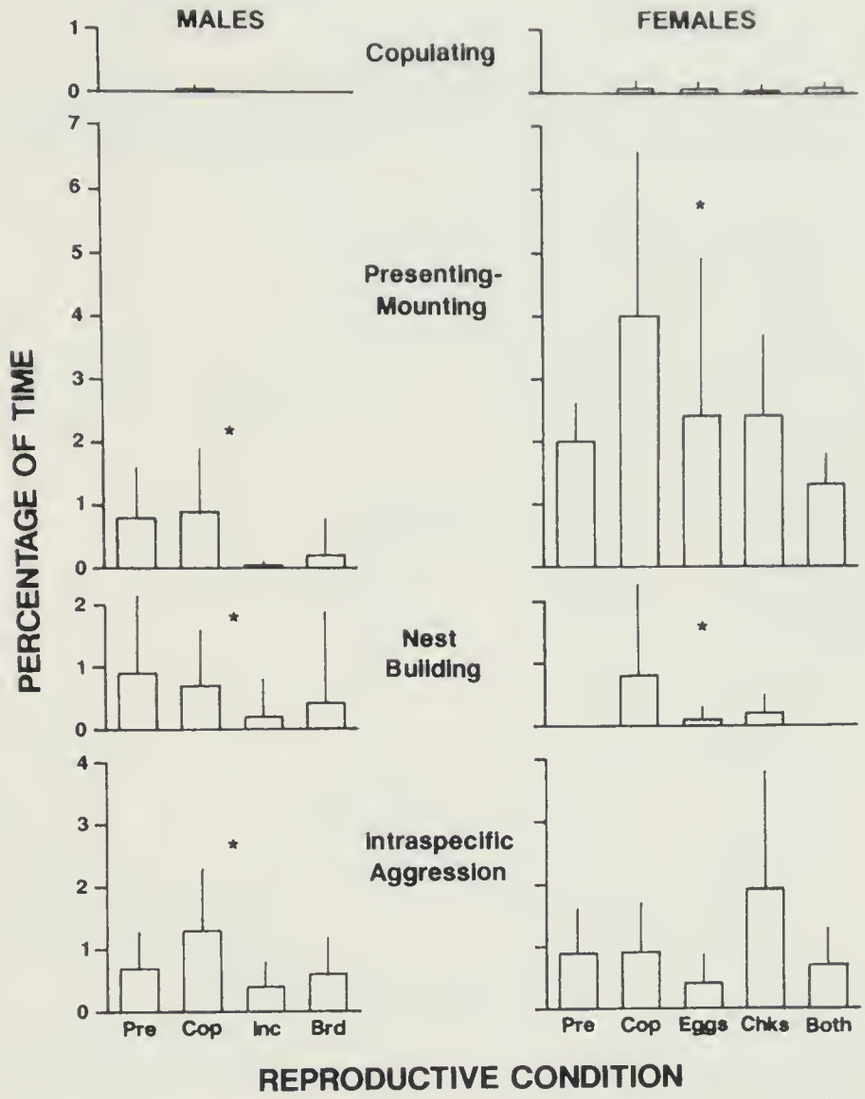

FIG. 2. Percentage of time males and females spent performing mating behaviors as a function of reproductive condition. Abbreviations, statistical significance, and sample sizes as in Fig. 1.

behavioral categories varied significantly with reproductive condition for both sexes (Figs. 1–3). Somatic behaviors consumed nearly 97% of the males' time prior to receiving a clutch (Fig. 1). Although never exceeding 3% of the males' time, mating behaviors occurred significantly more often prior to receiving a clutch, as would be expected (Fig. 2). Intraspecific aggression, highest in males during the copulation period, was primarily in defense of territory (Fig. 2).

Time budgets of males changed most drastically once eggs or chicks were present (Figs. 1–3). Males performed all observed incubation and most brooding, which occupied 39% and 26% of their time during the respective periods (Fig. 3). Males also did most of the walking-with-chicks (Fig. 3). Interspecific aggression, mostly directed at potential predators, was highest for brooding males (Fig. 3).

The increased time devoted to parental activities by males resulted in reduced time spent in most somatic activities (Fig. 1). Foraging time, in

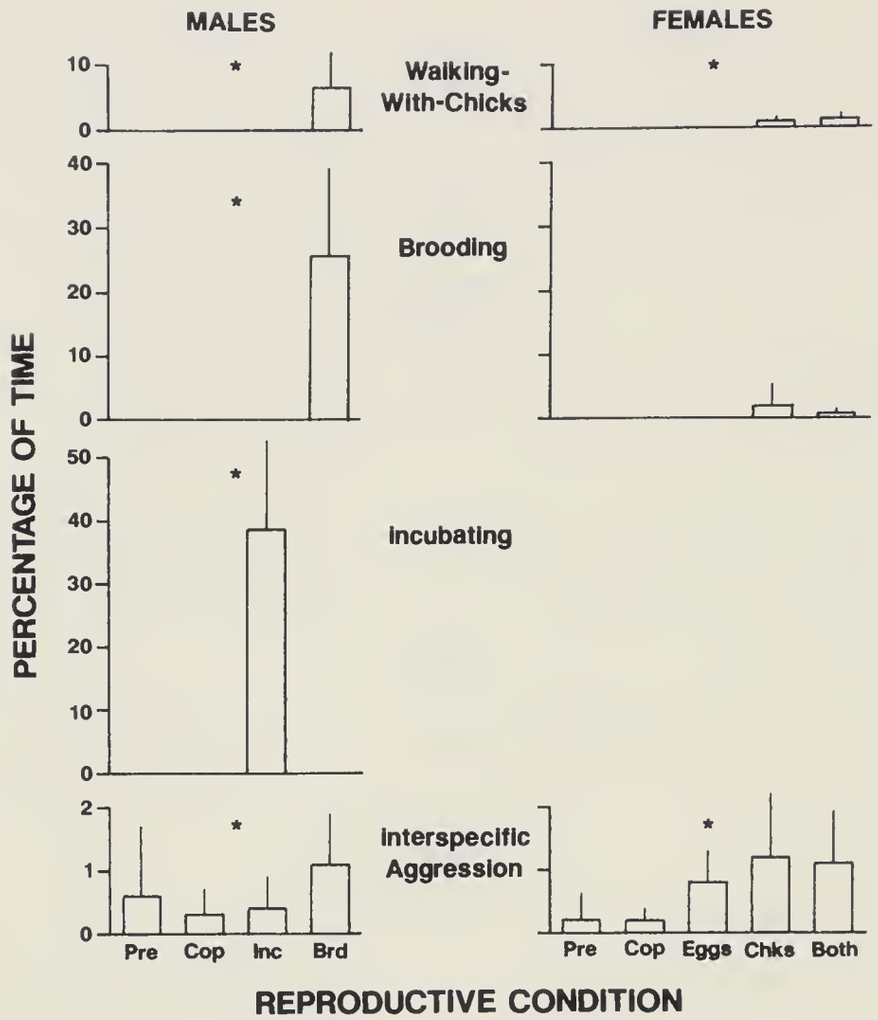

FIG. 3. Percentage of time males and females spent performing parental behaviors as a function of reproductive condition. Abbreviations, statistical significance, and sample sizes as in Fig. 1.

particular, decreased by about one-third during the incubation and brooding periods. Preening, resting, and walking also were less frequent (Fig. 1). Males sometimes foraged, preened, and rested in the vicinity of chicks, providing non-overt predator protection for the chicks as well as fulfilling somatic functions for the males.

The effects of change in reproductive condition on the time budgets of females were less obvious than for males. Mating behaviors were most frequent before males received clutches but continued between females and those mates not yet having eggs or chicks (Fig. 2). Female parental behavior was largely anti-predator in nature, although females occasionally brooded and walked-with-chicks (Fig. 3). Interspecific aggression by females was highest when at least one of their mates had eggs or chicks (Fig. 3). Foraging by females was high regardless of reproductive condition but decreased once chicks were present when resting and walking increased (Fig. 1). Like males, females also performed some of their somatic behaviors close enough to the chicks to help provide predator protection.

Sex differences.—The data in Figs. 1–3 were examined for differences between the sexes (Table 1); we judged the with-eggs-only and with-chicks-

TABLE 1

STATISTICAL SIGNIFICANCE OF SEX DIFFERENCES IN TIME BUDGETS DURING DIFFERENT REPRODUCTIVE CONDITIONS. VALUES ARE PROBABILITIES; NS = $P > 0.05$

Behavioral category	Reproductive condition			
	Pre-copulation	Copulation	Incubation/ with eggs only	Brooding/ with chicks only
N (male, female) =	16, 4	29, 19	16, 7	25, 7
Somatic behaviors				
Foraging	NS	NS	≤0.001	≤0.05
Preening	NS	≤0.05	≤0.01	≤0.05
Resting	≤0.05	NS	≤0.001	≤0.001
Flying	NS	<0.05	≤0.05	·NS
Walking	NS	NS	≤0.05	≤0.01
Mating behaviors				
Intraspecific aggression	NS	NS	NS	NS
Nest building	≤0.05	NS	NS	NS
Presenting-mounting	≤0.01	≤0.001	≤0.01	≤0.001
Copulating	—	NS	≤0.01	NS
Parental behaviors				
Incubating	—	—	≤0.001	—
Walking with chicks	—	—	—	≤0.001
Brooding	—	—	—	≤0.001
Interspecific aggression	NS	NS	NS	NS
No. of categories with significant differences	3/9	3/10	8/11	7/12

only periods of the females as most appropriate for comparison with the incubating and brooding periods, respectively, of the males. Prior to egg-laying the time budgets of both sexes were similar, differing only in low-frequency behaviors (flying, nest building, and presenting-mounting) or in low-energy-demanding behaviors (preening and resting).

However, once eggs or chicks were present the time budgets of males and females diverged greatly (Table 1). Males spent 39% of their time incubating while females were never observed incubating, and males brooded and walked-with-chicks 26% and 7% of the time, respectively, compared to only 2% and 1% for females with-chicks-only (Fig. 3). Conversely, incubating and brooding males spent significantly less time than females in most somatic behaviors (Table 1). Time spent in mating behaviors remained infrequent once eggs or chicks were present and did not differ significantly between the sexes, except that females continued copulating and presenting-mounting with their other mates (Fig. 3).

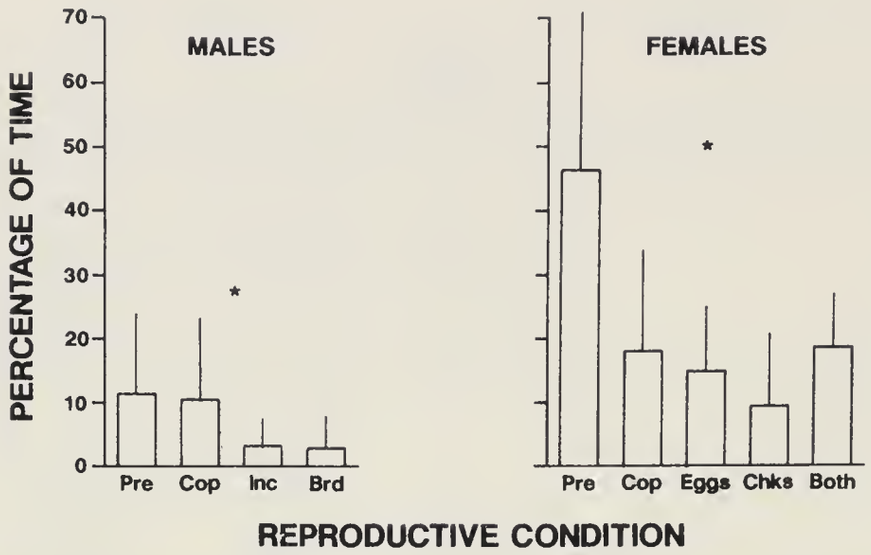

FIG. 4. Percentage of total time spent off the pond by males and females as a function of reproductive condition. Abbreviations and sample sizes as in Fig. 1. Statistical significance: * = $P \leq 0.05$ that there was no difference between reproductive conditions in the percentage of time spent off the pond.

Location differences.—Jacanas spent part of their time on nearby lawns or pastures (this study) or on meadows or grasslands (western Costa Rica, pers. obs.). Males spent much less time off the Turrialba pond once they had eggs or chicks (Fig. 4). Females spent nearly half their time off-the-pond during the precopulation period but significantly less time off-the-pond after that (Fig. 4).

Grouped behaviors were used to compare off-the-pond and on-the-pond time budgets. The percentage of time males and females spent foraging was significantly greater when off-the-pond than when on-the-pond during all reproductive conditions (Fig. 5). The inverse was always true for the other somatic behaviors (Fig. 5). The percentage of time the two sexes spent in intraspecific and interspecific aggression either did not differ significantly between off-the-pond and on-the-pond or else was significantly greater when on-the-pond (Fig. 5). No other mating or parental behaviors occurred off-the-pond during our observations.

The effect of location on the time budgets of females was much more complex than for the males. When females had males with eggs and/or chicks, the females distributed their time differently depending on which male's territory they were in (Fig. 6). Although females in all three reproductive conditions tended to feed a greater percentage of time when in territories of males without offspring than when in territories containing eggs or chicks, these differences were not significant (Fig. 6). The fact that females did not consistently reduce their foraging in territories with eggs or chicks also can be seen by examining the females' foraging patterns before and after laying the five clutches that eventually produced chicks

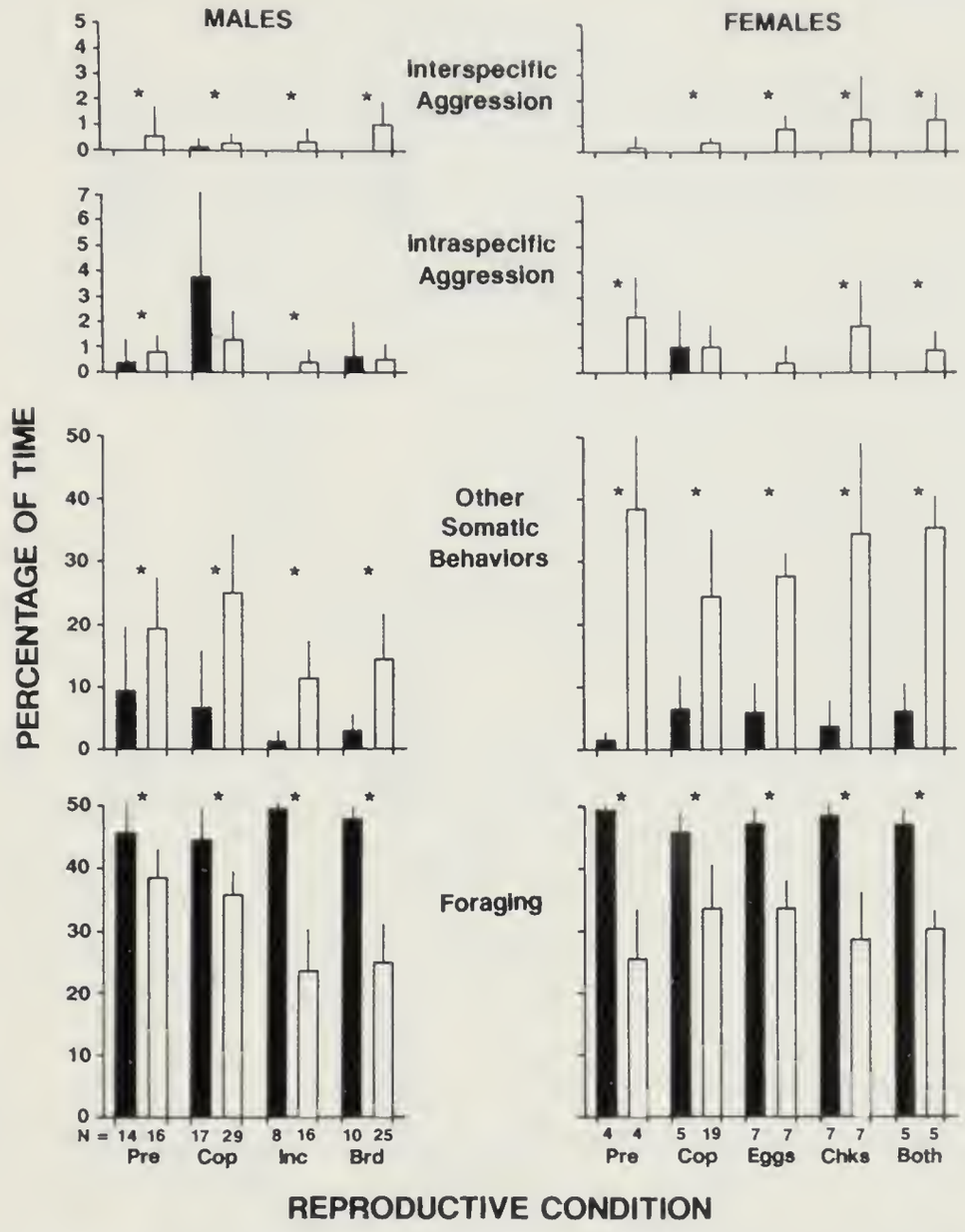

FIG. 5. Comparison of time budgets when males and females were in their territories (open bars) and when they were off the pond (solid bars). Abbreviations as in Fig. 1. Statistical significance: * = $P \leq 0.05$ that there was no difference between the percentage of time spent in a behavioral category when in their territories and the percentage of time spent in that category when off the pond.

(Table 2). The proportion of total female feeding time spent in the territory of the male who received the clutch did not change consistently from copulation throughout the nest cycle (Friedman two-way ANOVA; $\chi_r^2 = 1.2$, df = 2, $P = 0.691$).

Females in all three reproductive conditions spent significantly more time in other somatic behaviors when in territories containing eggs or chicks than when in territories with no offspring (Fig. 6). Preening and resting were the most frequent of these behaviors, and the tendency of females to perform them in territories containing eggs or chicks enabled the females to provide non-overt parental care in the form of predator

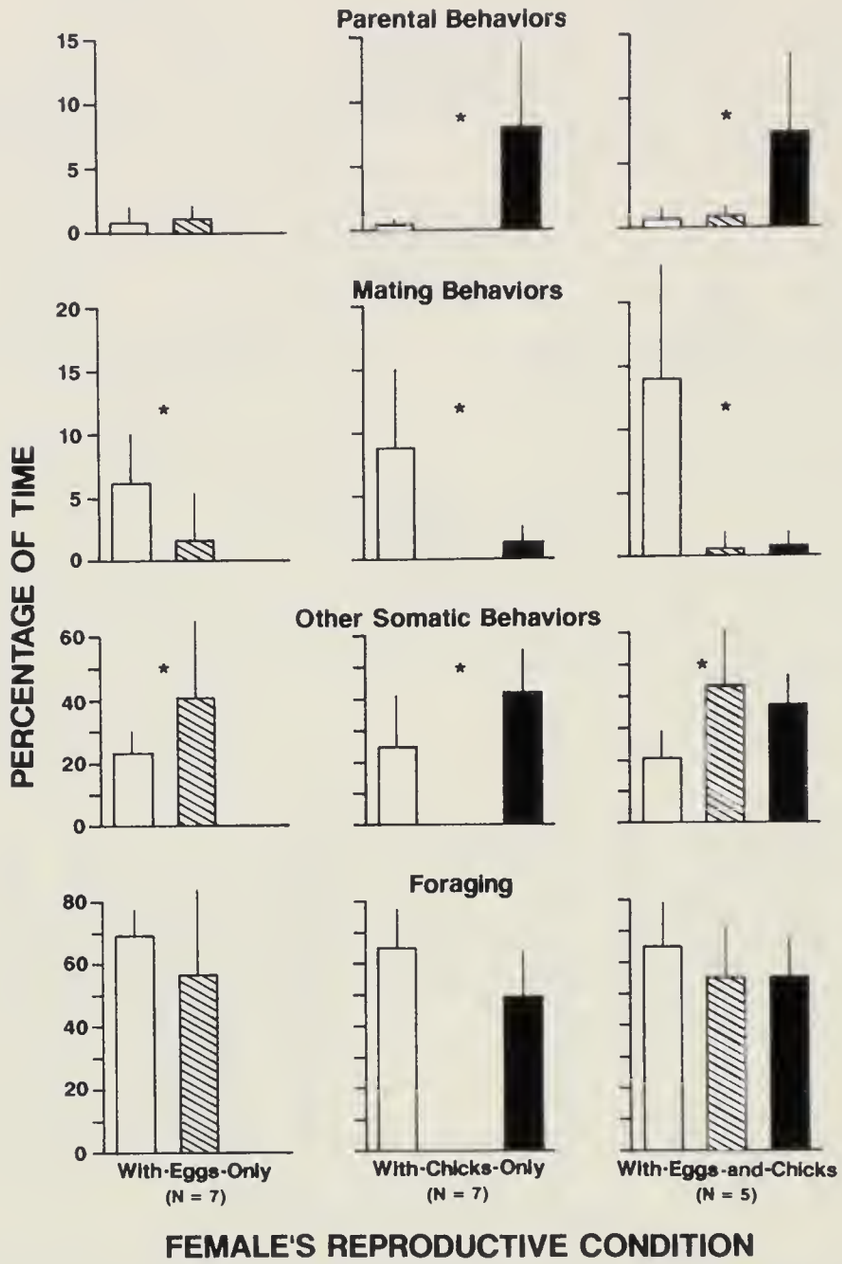

FIG. 6. Comparison of female time budgets during three reproductive conditions as a function of location. Open bars = in territory of male that had neither eggs nor chicks; hatched bars = in territory of male that had eggs; solid bars = in territory of male that had chicks. Statistical significance: * = $P \leq 0.05$ that there was no difference between the percentage of time females spent in a behavioral category when in territories of males in different reproductive conditions.

vigilance. As expected, mating behaviors were most frequent when females were in territories of males with no offspring, and parental behaviors were most frequent when females were in territories containing chicks.

Time of day differences.—Significant diurnal variation in time spent foraging occurred in all reproductive conditions for males (Fig. 7). During the precopulation and copulation periods, male foraging showed only slight mid-morning lulls. However, diurnal variation increased considerably in the incubation and brooding periods, with foraging peaking around midday (Fig. 7). Early morning and mid-to-late afternoon were

TABLE 2
PERCENTAGE OF TOTAL FEMALE FEEDING THAT WAS DONE IN TERRITORIES RECEIVING CLUTCHES THAT EVENTUALLY PRODUCED CHICKS

Clutch number	Clutch status					
	Copulation		Eggs present		Chicks present	
	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD
1	3	34.2 ± 14.5	3	41.0 ± 9.9	6	29.5 ± 16.4
2	6	33.6 ± 18.8	4	28.9 ± 9.8	1	58.8 ± 0.0
3	2	12.3 ± 2.6	2	42.2 ± 19.0	3	16.9 ± 3.2
4	5	5.7 ± 2.9	2	4.8 ± 3.7	4	9.0 ± 3.5
5	7	14.0 ± 10.7	1	27.5 ± 0.0	3	19.4 ± 11.0
Mean		20.0 ± 13.1		29.5 ± 15.7		26.6 ± 19.5

the coolest and rainiest parts of the daylight hours, respectively, and the times of greatest incubation and brooding (Fig. 7). The conclusion that parental demands, rather than changes in foraging efficiency, dictated the change in daily foraging pattern is supported by data for females, which were not observed to incubate, rarely brooded, and showed no significant diurnal variation in time spent foraging during any reproductive condition (Fig. 8).

In males, other somatic behaviors differed significantly with time of day during the incubation and brooding periods. Like foraging, these behaviors were less frequent early and late in the day as males devoted time to parental care (Fig. 7). Females exhibited no significant diurnal variation in time spent in other somatic behaviors during any reproductive condition (Fig. 8). Mating behaviors of both sexes showed significant diurnal variation during the copulation period, with the frequency of these behaviors generally being inversely related to the frequency of somatic behaviors (Figs. 7 and 8).

DISCUSSION

The mating system of the Northern Jacana is an example of resource defense polyandry (Emlen and Oring 1977) in which females gain access to several males by excluding other females from the males' territories. Pair formation in this species is much less a product of intersexual courtship than it is a product of intrasexual competition for territories. Males compete among themselves for breeding territories and females compete among themselves for control over the males and their territories. A male accepts as his mate the female who excludes other females from his territory, and females pair with males that hold territories within her ter-

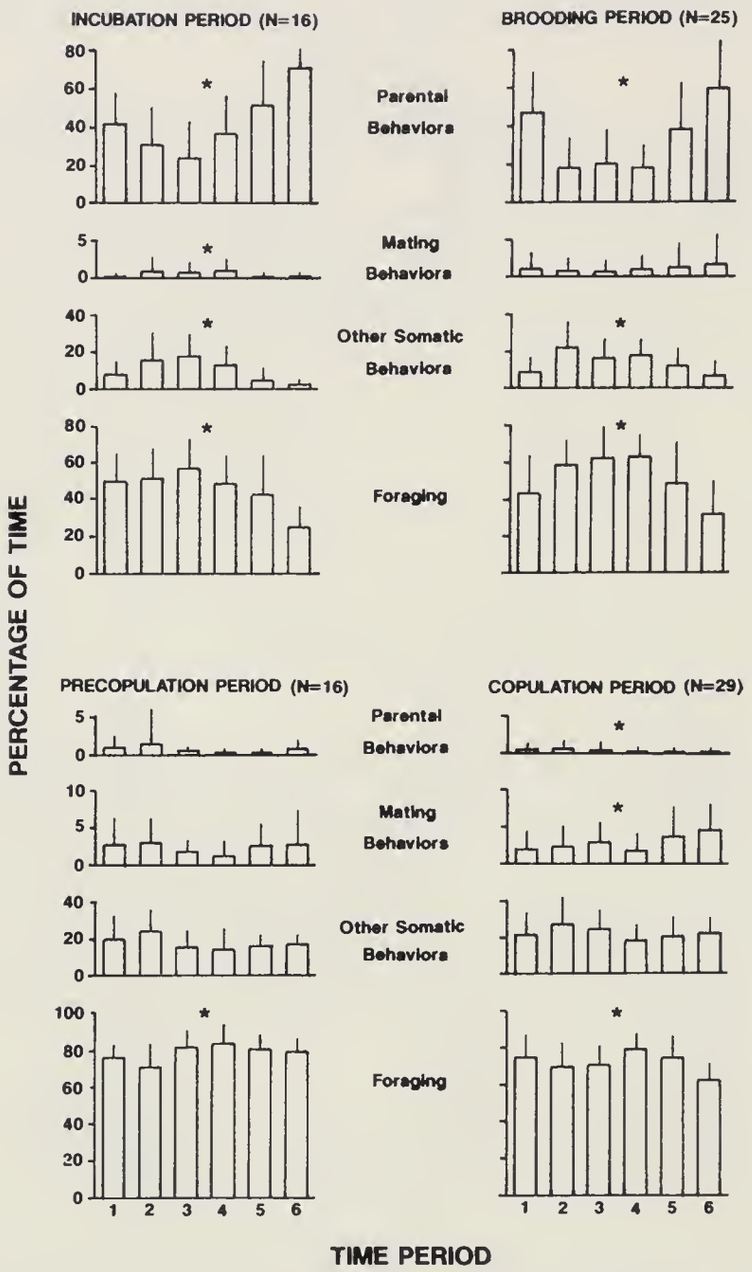

FIG. 7. Male time budgets during four reproductive conditions as a function of time. Time periods: 1 = dawn–08:00, 2 = 08:00–10:00, 3 = 10:00–12:00, 4 = 12:00–14:00, 5 = 14:00–16:00, 6 = 16:00–dusk, CST. Statistical significance: * = $P \leq 0.05$ that there was no difference between time periods in the percentage of time spent in a behavioral category.

ritory. At Turrialba, Northern Jacanas held territories throughout the year and their ownership changed infrequently. Except during these infrequent ownership changes, such a system ought to require little time expenditure devoted to mating behaviors, an hypothesis that is confirmed by our data. Neither males nor females spent more than 2% of their time in intraspecific aggressive encounters (Fig. 2). For both sexes, the majority of these encounters occurred in territories of males with neither eggs nor chicks, probably as a consequence of males wandering more widely when they were not incubating or brooding. Presenting-mounting and copulating consumed less than 1% of male time budgets and 4% or less of female

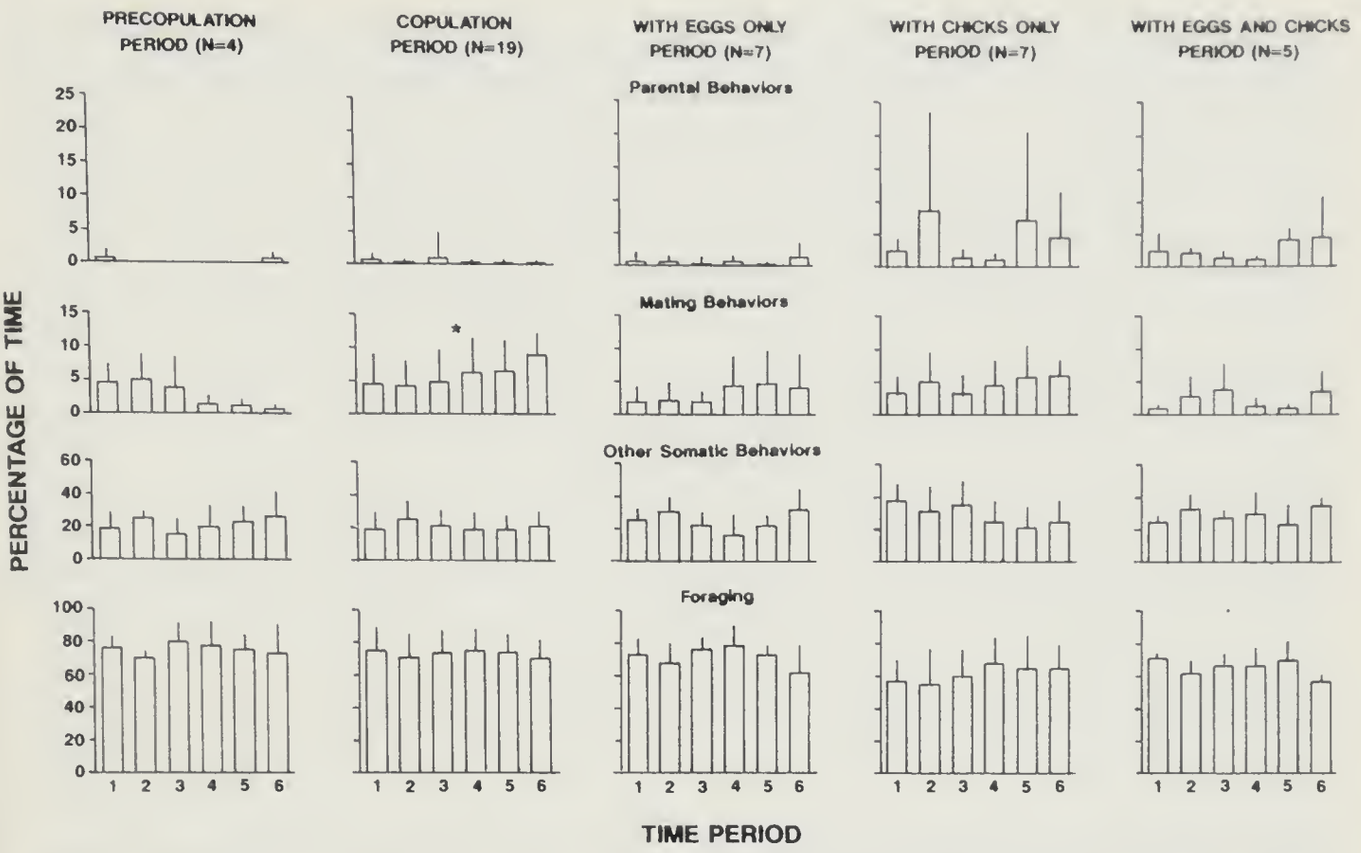

FIG. 8. Female time budgets during five reproductive conditions as a function of time. Time periods and statistical significance as in Fig. 7.

time budgets, with the peaks occurring as expected during the precopulation and copulation periods (Fig. 2).

The evolution of sexual differences in parental investment is prerequisite to the evolution of polygamy (Trivers 1972, Maynard Smith 1977). Polyandry should evolve when males can increase their fitness by assuming the bulk of parental duties while the female is free to regain the nutrient and/or energetic ability to produce replacement clutches (Emlen and Oring 1977). Thus, male and female jacanas should have different reproductive strategies that ought to be reflected as major differences in their time budgets, particularly in the time devoted to energy acquisition and parental duties.

Male foraging was high throughout the day during the precopulation and copulation periods, but once eggs or chicks were present the demands of incubating, brooding, and attending chicks resulted in greatly reduced foraging, particularly early and late in the day (Figs. 1 and 7). This reduction was associated with a decrease in time spent off-the-pond, most of which had been devoted to foraging (Figs. 4 and 5).

This decrease in male foraging probably had little effect on male fitness during the peak of breeding. Even with reduced time spent foraging during parts of the day, males seemed able to satisfy their energy needs during

the four weeks of incubation and 10 weeks of brooding. However, the presence of eggs or young chicks at times of the year with extensive rainy periods and cooler temperatures may require so much time incubating and brooding that the male has insufficient time to forage. It was during such weather conditions that females "reluctantly" brooded (the chicks usually had to force their way under the female's wings) and one male lost a set of chicks less than one week old because of his inattentiveness (Jenni and Betts 1978). These chicks hatched during an extensive rainy period; two disappeared after five days for unknown reasons, and the other two were preyed upon by a Purple Gallinule (*Porphyrula martinica*) while the parents were both away from the pond. The fact that several territorial birds seemed to be spending more time foraging off-the-pond than usual suggests that food abundance was relatively low on-the-pond, perhaps also because of the weather conditions. Low food availability on-the-pond may have produced a conflict in the male's time budget between his foraging needs and the parental care needed by his offspring, with the latter getting less than necessary. Certainly, it would be adaptive in such cases for the male to provide for his own survival needs in preference to those of his chicks, which could not have survived without him anyhow.

The foraging patterns of males and females differed in several ways. Female foraging remained high throughout the day regardless of reproductive condition and was highest during the precopulation, copulation, and with-eggs-only periods when the energetic demands of egg formation should be highest. Thus, while male foraging is reduced by parental duties, females can continue to acquire energy and nutrients for additional clutches. That this is potentially beneficial to the male is evidenced by the history of one male who received three clutches in 1974. Although he abandoned his first clutch when his mate was replaced, his new mate provided him a clutch two months later. This clutch was lost before hatching, and he received a replacement clutch within two weeks.

Another important aspect of female foraging is the amount of foraging done in territories containing chicks. A potential benefit of polygamy is reduced competition between adults and offspring for food if the polygamous parent abandons the territory (Pitelka et al. 1974). Female jacanas are significantly larger than males (Jenni and Collier 1972) and have greater metabolic maintenance demands, which may contribute to the greater foraging time observed in females of this species. When food abundance is low, which by circumstantial evidence seemed to occur at irregular intervals at Turrialba, it would seem appropriate for females to concentrate foraging elsewhere rather than in territories with chicks. Although females did forage a smaller proportion of the time they were in territories with chicks (Fig. 6), they also spent more total time in these

territories. Thus, there was no overall reduction of foraging, at least in the territories of the five broods produced during this study (Table 2). A reduction in foraging and hence in competition may occur when food abundance is low, but we have no data to test this possibility.

The male is responsible for the majority of parental care. Once he received a clutch, a male's daily time budget changed to include extensive periods of incubation, brooding, and walking with the chicks (Fig. 3), especially during the cool early mornings and often rainy late afternoons (Fig. 7). There was generally a corresponding decrease in the frequency of male foraging, other somatic behaviors, and time spent off-the-pond (Figs. 4 and 7). By spending more time on-the-pond, the male probably provided the eggs and chicks better protection from potential predators.

The females' reproductive strategy is one of providing eggs and predator protection. High levels of foraging allowed for the former and spatial variation in the performance of a variety of behaviors allowed for the latter. Females concentrated preening, resting, and walking in territories with offspring (Fig. 6). In choosing these territories for these maintenance behaviors, the females provide the potential for predator protection, and this may have been largely responsible for the involvement of females in so many interspecific aggressive encounters in territories containing chicks (Fig. 6).

Of the various hypotheses for the adaptiveness of classical polyandry, our data best support the replacement clutch hypothesis for polyandry in the Northern Jacana, although they are insufficient by themselves to eliminate other hypotheses completely. Clutch loss in the Turrialba population was high, as predicted by this hypothesis. Based on 1–2 month observations of this population between 1963 and 1973, Jenni (1974) estimated nesting success at 50% or less. Four of eight clutches laid in 1974 were lost before or soon after hatching, and only one chick from each of the other clutches remained by the end of the study. Osbourne (1982) reported total clutch loss in 84.6% of 52 Wattled Jacana nests. Although temperate zone, polyandrous Spotted Sandpipers had a hatching success of only 39% over nine years (Oring et al. 1983), tropical shorebirds, in general, experience lower nesting success and greater replacement opportunity than more northern species (Erckmann 1983).

Inherent in the replacement clutch hypothesis is the assumption that polyandrous females, freed from most parental duties, can rapidly replace lost energy stores and lay additional clutches. However, this assumption cannot be tested simply by comparing clutch replacement rates between polyandrous and monogamous, biparental species. Although a female may be physiologically capable of producing another clutch, doing so may be delayed by such factors as a change of mates, territorial challenges from

other females, and weather variations. In Spotted Sandpipers the laying rate of additional clutches was affected by the rate of nest predation and the availability of males but not by food abundance, and females were able to begin replacing clutches as soon as the day after a clutch was lost (Lank et al. 1985).

Comparison of clutch replacement rates between polyandrous and monogamous, biparental shorebirds is further clouded by the possibility that rapid replacement also may be important to monogamous species. Killdeers suffer clutch losses as high as 64% (Mace 1971), and females spend significantly less time in parental duties and more time foraging than males (Brunton 1988). This may enhance production of additional clutches; Killdeers renest up to three times in a season (Mundahl 1982, Brunton 1988). Males of other monogamous shorebirds also contribute significantly more time to parental duties than females even though biparental care is necessary (Hussell and Page 1976, Miller 1985), but whether this is related to the rate of clutch replacement is not known.

In this study, we have clutch replacement data for only one renesting; the new clutch was started 19 days after the female started the first clutch and 15 days after its loss. One female Wattled Jacana laid four clutches for the same male over a 45-day period (Osbourne and Bourne 1977), and another laid six clutches for two males over a 60-day period (Osbourne 1982). The shortest replacement time was 10 days after starting the first clutch and only two days after the first clutch disappeared. Thus, replacement time varies considerably within the tropical jacanas, and we do not believe knowledge of the factors producing this variation is sufficient at this time to rule out the replacement clutch hypothesis on the basis of a comparison of replacement times of polyandrous and monogamous females.

Conversely, the replacement clutch hypothesis is supported by our female foraging time data. This hypothesis predicts that time spent foraging by females should be higher than for males and should be higher than in species which usually lay only one clutch per season. The first prediction is met by our data. Although initially similar, time spent foraging by males and females became significantly different after laying as male foraging time decreased by one-third (Fig. 1). Comparison with other species is not possible because we have no data on food abundance which can affect time spent foraging (Maxson and Oring 1980).

The female energetic stress hypotheses for the adaptiveness of polyandry suggest that severe energy stress of the female makes her more likely to desert the male than help with parental care (Lenington 1984). But Erckmann (1983) and Maxson and Oring (1980) argue that food scarcity should select for biparental incubation rather than desertion by either parent,

and female Spotted Sandpipers did not incubate less when food was scarce (Maxson and Oring 1980, Lank et al. 1985, Oring and Lank 1986). Our data do not support these hypotheses for the Northern Jacana. First, the rare occurrences of female brooding occurred just when food was least abundant. Second, female foraging time decreased after laying (Fig. 1), rather than increasing as predicted by this hypothesis (Lenington 1984). Third, our females increased resting time after laying (Fig. 1).

The uniparental care hypotheses also are not supported by our data for the Northern Jacana. Females did not reduce the absolute amount of time they fed in a territory once eggs or chicks were there (Table 2). However, this observation is based on the history of only five clutches, and we do not have corresponding quantitative data on food supply.

The limited amount and incompleteness of published data make rigorous testing of these hypotheses difficult at best. Furthermore, there are not yet sufficient data available to conclude that the various mating systems identified as polyandrous are in fact identical (Oring 1986). Attempting a single explanation for the adaptiveness of classical polyandry is premature before we know we are dealing with a single type of mating system. Clearly we need more descriptive data on the understudied, presumptively polyandrous species.

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TIME-ACTIVITY BUDGET OF WILSON'S AND SEMIPALMATED PLOVERS IN A TROPICAL ENVIRONMENT

Alain Morrier and Raymond McNeil[1]

Abstract.—We compared seasonal variations in the daylight activity budget of Semipalmated (*Charadrius semipalmatus*) and Wilson's plovers (*C. wilsonia cinnamominus*) in northeastern Venezuela. The former are Nearctic migrants which use the area as a migratory stop-over and wintering area; the latter are residents and breed in the region. Feeding, resting, and aggressive manifestations are the three main activity categories. The seasonal activity patterns of the species differ. In both species, the seasonal pattern of time spent resting is the inverse of that for feeding. From October to April, Semipalmated Plovers fed during most of their daylight time in spite of a decrease in feeding in January and February. In contrast, Wilson's Plovers devoted more time to resting than to feeding from November to April (the non-breeding period). In both species, the seasonal variations in the time spent feeding during daylight can be explained by variations in their energetic needs, e.g., for molting and building fat reserves. Time devoted to aggression was very low in both species but increased in March–April for Wilson's Plovers, just before the beginning of reproductive activities. Daily energy expenditure and energy intake were estimated for Wilson's Plovers, supposing that they were resting from dusk to dawn. From November to March, daylight feeding alone was insufficient to counterbalance energy expenditure, indicating that they foraged primarily during nighttime. *Received 14 Jan. 1991, accepted 6 June 1991.*

Some migratory shorebirds continue accumulating fat reserves during the few weeks following their arrival in coastal habitats of northern South America before departing for regions farther south (McNeil 1970a). From about November to February, shorebirds lose weight before starting to deposit large fat reserves in March–April in preparation for their northward migration to the breeding grounds (McNeil 1970a). This occurs commonly in migratory species within the genera *Charadrius, Pluvialis, Tringa, Limnodromus,* and *Calidris* which breed in northernmost North America. However, some shorebirds (e.g., Wilson's Plover [*C. wilsonia*] and Black-necked Stilt [*Himantopus mexicanus*]) are sedentary and permanent residents in the Neotropical region, and share tropical environments together with species migrating from the Nearctic region (McNeil et al. 1990). These Neotropical residents, contrasted to migrants, have only small fat reserves which are made up immediately before the breeding season or just before a food-shortage period (McNeil 1970b, 1971).

Myers and McCaffery (1984) suggest that the frequency and duration of the food intake in migratory species should vary seasonally. For ex-

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ample, birds must eat when (1) refueling at a stop-over place after a long non-stop over-sea flight, (2) molting, or (3) accumulating fat in preparation for migration. In contrast, for allied or congeneric species residing the entire year in the Neotropical region, seasonal variations in the energy intake should be less. The food intake should be higher at the beginning of the breeding season than in the other periods. Little is known concerning the activity budget of shorebirds wintering or residing in tropical environments. The only available data from regions of high temperatures were provided by Puttick (1979) for the Curlew Sandpiper (*Calidris ferruginea*) in South Africa, Hockey (1984) for the African Black Oystercatcher (*Haematopus moquini*), and Maron and Myers (1985) for the Sanderling (*C. alba*) in California. In addition, Zwarts et al. (1990) have shown that the lowest feeding activity in nine of 14 Palearctic shorebird species wintering in Mauritania was observed in February and that the activity was at a maximum in March–April.

In this paper we compare the seasonal variations in the daylight activity budget of Semipalmated (*C. semipalmatus*) and Wilson's plovers in a tropical environment. The former breeds in North America and winters from southern United States to southern South America (Hayman et al. 1986). There are three subspecies of Wilson's Plovers: *C. w. wilsonia, C. w. beldingi,* and *C. w. cinnamominus* (Hayman et al. 1986). The race *cinnamominus* is a permanent resident of the Caribbean, the Atlantic coast of northern South America from Colombia to northeastern Brazil, and the islands off Venezuela in the Caribbean Sea. The Semipalmated Plover and the Wilson's Plover (*cinnamominus*) occur together on the coast of northern South America, in particular in the coastal lagoons of Venezuela (McNeil et al. 1990). The seasonal variations in the fat content of both species were documented by McNeil (1970a, b). After a preliminary analysis of the data on the daylight activity budget of Wilson's Plovers, we examined seasonal variations of its daily energy budget. The same approach was not possible for the Semipalmated Plover since it was almost impossible to collect data on the size and identity of its prey.

STUDY AREA AND METHODS

The study was done in the Chacopata lagoon complex (10°41′N, 63°46′W) on the north side of the Araya Peninsula, State of Sucre, in northeastern Venezuela. Up to 300 Semipalmated Plovers have been observed in August and September at Chacopata during fall migration (Limoges 1987). Their average number decreases to 100 individuals from the end of October to December and increases to about 250 birds between January and April. Spring migration occurs at the end of April and the beginning of May (Limoges 1987). The population of Wilson's Plovers is highest in August–September (around 100 birds) and decreases to about 10–20 birds in October due to post-breeding dispersal and regional movements.

The breeding population is about 50 individuals. Pair formation and the beginning of breeding activities occur in March–April (Limoges 1987).

Semipalmated and Wilson's plovers were observed from 18 October 1985 through 20 April 1986. All observations were made using a 20× spotting scope and 7 × 28 binoculars. Their activities were recorded using focal sampling procedures (Altmann 1974) during 15-sec intervals. Activities were grouped under six functional categories: (1) feeding—pecking at substrate, walking and running in pursuing prey, waiting or pausing while hunting prey, eating prey, drinking, and foot-tapping; (2) resting—motionless, huddled on the dry mud or on sand, sleeping with head tucked in plumage, often standing on one leg; (3) aggression—ground or aerial chases, fights, ground or aerial escape, ground displays, alert due to agonistic interactions; (4) preening—preening, bathing, and comfort movements; (5) locomotion—walking, running, and flying not associated with foraging, aggression, or being alert; (6) being alert—aerial escape of a predator or flying for an unknown reason, low crouching posture, and other alert movements (e.g., head-bobbing). Only one bird was observed at a time, and for as long as possible. When it was lost from sight, another one was selected. We were unable to collect data on the Wilson's Plover in the second half of December and February, and the first half of April, and on the Semipalmated Plover in the first half of January and April.

We tried to sample the duration of total daylight period every two weeks by observation periods of 1–12 h distributed over sampling sessions of 1–5 consecutive days (Tables 1 and 2). However, the plovers were sometimes momentarily out of sight. Consequently, as a measure of the relative importance of the time devoted to each activity category during the total daylight period, we calculated a daylight time-activity index (TAI) per session

$$TA_iI\ (\%) = \frac{TTA_i \times 100}{TDO} \qquad (1)$$

where TTA_i = total time (min) spent in a given activity category (i) during the sampling session, and TDO = total duration of the observations (min) during the sampling session (Tables 1 and 2). Time-activity indices (TA_iI) of the two plovers were compared, for each activity category, with the Student *t*-test.

Equation (1) gives a single value of TA_iI per activity and per sampling session. With single values per sampling session, statistical analysis of the seasonal variation in the time devoted to a given activity is not feasible. Therefore, the duration of the daylight period of the middle day of each sampling session (each sampling session lasted between 1–5 consecutive days; Tables 1 and 2) was divided into 24 intervals of equal duration. In order to measure the relative importance of the time devoted to each activity category during each interval, we calculated a time-activity index per interval (TAII) as follows:

$$TA_iII\ (\%) = \frac{TTA_iI \times 100}{TDOI} \qquad (2)$$

where TTA_iI = total time (min) spent in a given activity category (i) during the interval, and TDOI = total duration of the observations (min) during the interval.

We used ANOVA to test the statistical significance of the variance of the TA_iII values between the different daylight periods for each activity category. Daylight periods were then compared *a posteriori* with Duncan's multiple range test (Scherrer 1984). One exception was for the time-aggression indices ($TAI_{ag}I$) of the Wilson's Plover which were divided *a priori* into two time periods: (1) from October to February and (2) the beginning of the breeding period (March–April). Both periods were compared by the use of the Student *t*-test.

TABLE 1

SAMPLING CALENDAR OF SEMIPALMATED PLOVERS GIVING, FOR EACH SESSION, THE DURATION OF THE DAYLIGHT PERIOD, THE TOTAL DURATION OF THE OBSERVATION, THE PERCENTAGE OF THE DAYLIGHT PERIOD COVERED BY OBSERVATIONS, AND THE TOTAL NUMBER OF BIRDS OBSERVED

Sampling sessions	Duration of the daylight period (h:min)	Total duration of observations during the sampling period (h:min)	Percentage of the daylight period covered by observations	Total number of birds observed
25–26 October	11:50	8:06	68.42	28
11–13 November	11:44	8:10	69.75	28
22–24 November	11:36	7:17	62.82	33
4–6 Deeember	11:33	7:21	63.74	21
13–17 December	11:31	7:22	63.74	11
20–24 January	11:33	9:22	81.10	18
3–4 February	11:43	10:07	86.34	25
19–20 February	11:50	8:59	75.92	34
16–18 March	12:04	8:29	68.96	9
27–31 March	12:07	8:30	70.15	31
16–20 April	12:22	8:56	72.34	33

The daily energy expenditure (DEE; 24-h, ineluding the night) for free-living Wilson's Plovers was estimated by summing the time spent in each activity, such as foraging and walking, times the ealorie equivalent of eaeh eategory, as follows (King 1974):

$$DEE = \Sigma(T_i K_i BMR) \quad (3)$$

where T_i = time spent (min) in the activity eategory i, K_i = inerement faetor, as multiple of the BMR, alloeated to eaeh aetivity eategory (i) (Table 3), and $BMR = 0.0808W^{0.734}$ (Asehoff and Pohl 1970), where BMR is the basal metabolie rate in kJ/h and W is the average body mass (g) of individuals eaptured monthly in the Chaeopata lagoon. For eaeh daylight period, the energy intake (EI) of Wilson's Plovers was ealeulated using the following formula (adapted from Puttiek 1980):

$$EI = \Sigma[(T_f R_f n_i)(m_i e_i A)] \quad (4)$$

where T_f = total daylight time spent foraging (min), R_f = mean rate of foraging (mean number of prey taken/min), n_i = pereent of ith prey item in diet, m_i = dry mass of organie matter of ith prey item (g), e_i = energy eontent of ith prey item (kJ/g of dry mass), and A = assimilation efficiency = 0.65 (as determined for *Uca tangeri* by Zwarts and Blomert [1990]).

Small fiddler crabs (*Uca thayeri*) comprised 98.6% of Wilson's Plover prey. The plovers were observed catching very small, unidentified, other prey types only on four other oeeasions. Size estimates of crabs were based on the carapaee width of the erabs in comparison with plover bill lengths. Thus, prey items (i) differed only in size, not in speeies. Undamaged erabs of different sizes were colleeted and the maximum width of their earapaee was measured to the nearest 0.1 mm. They were dried at 60°C for 8–12 h, and the dry mass (m_i) was determined to 0.001 g. Energy content (e_i) of different crab sizes was obtained with a Phillipson's microbomb calorimeter. Sulphide and nitrate eontents were negligible and were

TABLE 2

SAMPLING CALENDAR OF WILSON'S PLOVERS GIVING, FOR EACH SESSION, THE DURATION OF THE DAYLIGHT PERIOD, THE TOTAL DURATION OF THE OBSERVATION, THE PERCENTAGE OF THE DAYLIGHT PERIOD COVERED BY OBSERVATIONS, AND THE TOTAL NUMBER OF BIRDS OBSERVED

Sampling sessions	Duration of the daylight period (h:min)	Total duration of observations during the sampling period (h:min)	Percentage of the daylight period covered by observations	Total number of birds observed
18–21 October	11:52	8:36	72.47	12
11–12 November	11:44	7:28	63.67	13
21–22 November	11:36	9:25	78.92	6
1 December	11:34	10:21	86.64	6
14–16 January	11:35	11:01	95.11	8
29–30 January	11:40	10:17	88.14	14
15–17 February	11:48	11:10	94.70	7
8–9 March	11:59	11:06	92.63	7
22–24 March	12:08	11:13	92.45	8
11–13 April	12:19	10:10	82.54	16

not taken into account in calculating the energy content. Results were expressed in terms of kJ/g of dry mass. A correction (i.e., 0.6 kJ/g of $CaCO_3$) was made for the endothermic reaction during the combustion caused by decomposition of $CaCO_3$. Based upon data of Zwarts and Blomert (1990) for *U. tangeri,* the $CaCO_3$ content of *U. thayeri* was estimated equal to 30% of their dry mass.

Wilson's Plovers were mist-netted at monthly intervals and weighed to the nearest gram.

TABLE 3

VALUES FOR THE K-FACTORS ALLOCATED TO EACH ACTIVITY CATEGORY IN CALCULATING DAILY ENERGY EXPENDITURE OF WILSON'S PLOVERS

Activities	kJ/h	References
Foraging	2.0	Orians 1961
Resting	1.24	King 1974
Preening	1.8	Wooley and Owen 1978
Flight[a]	12.0	King 1974
Walking	1.7	Wooley and Owen 1978
Fight	15.2	Maxson and Oring 1980
Ground display	4.0	Maxson and Oring 1980
Alert[b]	3.4	Maxson and Oring 1980
Running[c]	2.0	Fedak et al. 1977
Nocturnal resting	1.25	King 1974

[a] Including all flights associated with alert reactions, agonistic manifestations, and locomotion.
[b] Including alert reactions associated with aggressiveness, but excluding flight escape.
[c] Including running for feeding, or ground pursuit and escape.

RESULTS

Daytime activity budget.—Except in January and February, feeding was the principal activity of Semipalmated Plovers and accounted for an average of 60.0% ± 13.9 of their time (Fig. 1). Percentage of time devoted to foraging varied significantly during the study period ($F = 7.61$, $P < 0.001$). October, December, and March–April were characterized by time-foraging indices ranging from 68.6–86.1%, while in November and January–February foraging ranged from 31.7–46.7% of the day. Significant differences in the fraction of daylight hours spent feeding took place between October and November, November and December, December and January, and finally between February and March. In contrast, time devoted to feeding by Wilson's Plovers averaged only 17.0% ± 12.5, but showed significant seasonal variations ($F = 9.17$, $P < 0.0001$) with values for the time-foraging indices of 55.0 and 42.7% for the end of October and the beginning of April, respectively, and ranging from 1.2 to 15.4% from November to March (Fig. 1). Foraging was the principal activity of Wilson's Plovers only at the end of October.

Semipalmated Plovers, consistently and significantly, devoted more time to feeding than Wilson's Plovers ($t = 5.12$, $P < 0.0001$).

Wilson's Plovers rested significantly more during their daylight period (average = 77.8% ± 12.6) than Semipalmated Plovers (average = 29.0% ± 13.5; $t = 5.88$, $P < 0.001$). In both species, time spent resting showed significant seasonal variations ($F = 8.05$, $P < 0.0001$ for the Semipalmated Plovers; $F = 7.51$, $P < 0.0001$ for Wilson's Plovers) and followed a pattern strictly inverse of the time spent feeding (Fig. 2). Time devoted by Semipalmated Plovers to agonistic behavior was always extremely low (average = 0.1% ± 0.1; Fig. 3), except at the end of October when their time-aggression index (0.7%) was significantly higher than in other periods ($F = 2.97$, $P < 0.01$). However, during three consecutive days at the beginning of October, one color-banded bird was observed regularly directing agonistic activity towards conspecific intruders while defending a feeding territory. During the same period, another individual defended an adjacent territory. The former was never seen in the lagoon thereafter; it was likely a bird in transit to other regions farther south. Interspecific interaction involving Semipalmated Plovers was noted only twice, in March, when two individuals forced a small peep sandpiper (*Calidris* sp.) out of their feeding area.

Aggression accounted, on average, for only 0.6% ± 0.4 of the daylight time-budget of Wilson's Plovers (Fig. 3) but increased significantly in March–April (1.2 to 1.6%) in comparison with other months (0.02–0.5%; $t = 3.72$, $P < 0.01$). As for Semipalmated Plovers, agonistic manifestations

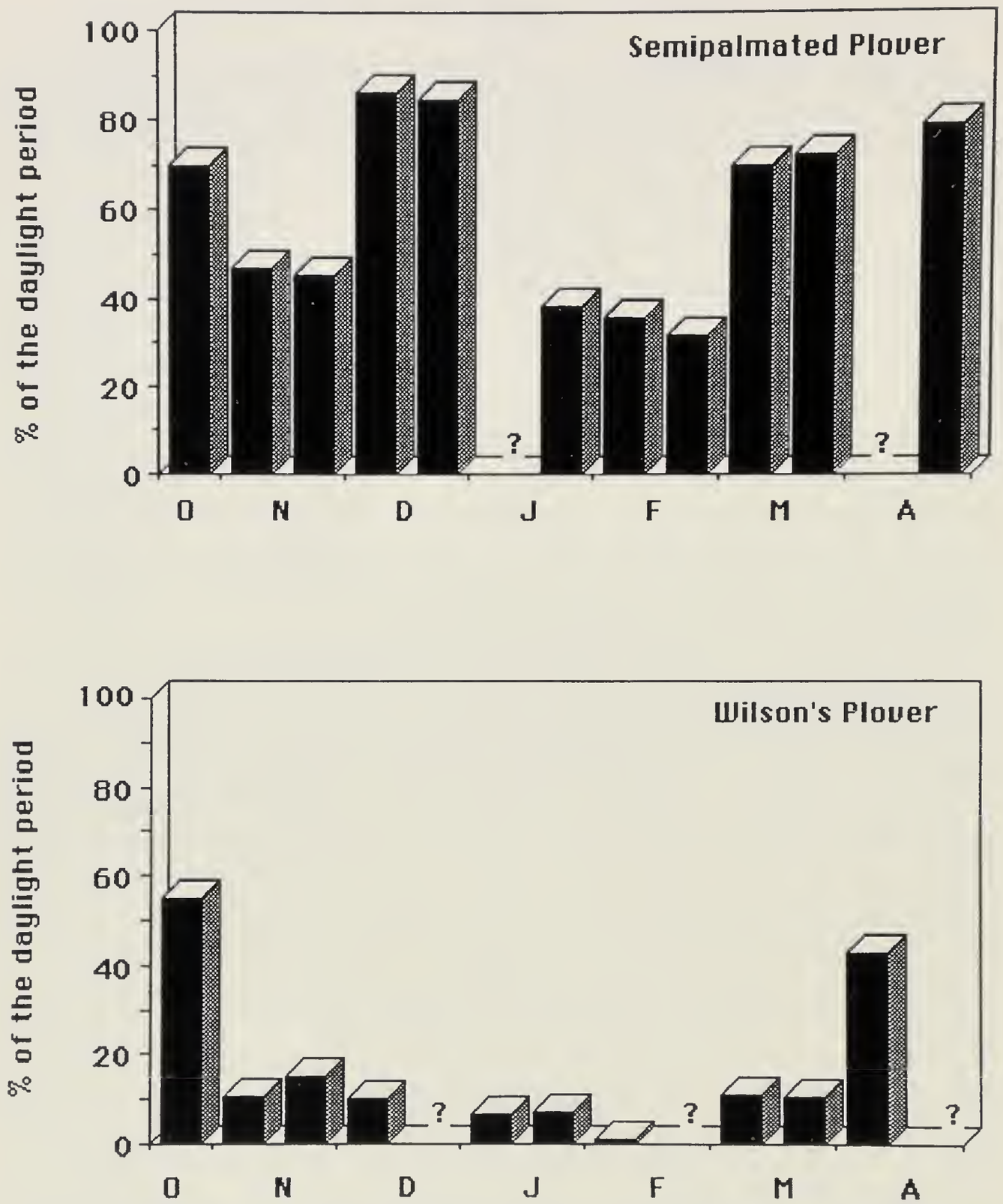

FIG. 1. Seasonal variations in the relative importance of time devoted to feeding during the daylight period. Interrogation marks (?) indicate the absence of data.

of Wilson's Plovers were strictly intraspecific except in two cases: in November, one individual chased a Semipalmated Plover from its resting area and at the beginning of March another one displaced a feeding Short-billed Dowitcher (*Limnodromus griseus*).

Wilson's Plovers devoted significantly more time to aggression than did Semipalmated Plovers ($t = 2.46, P < 0.05$) except at the end of October

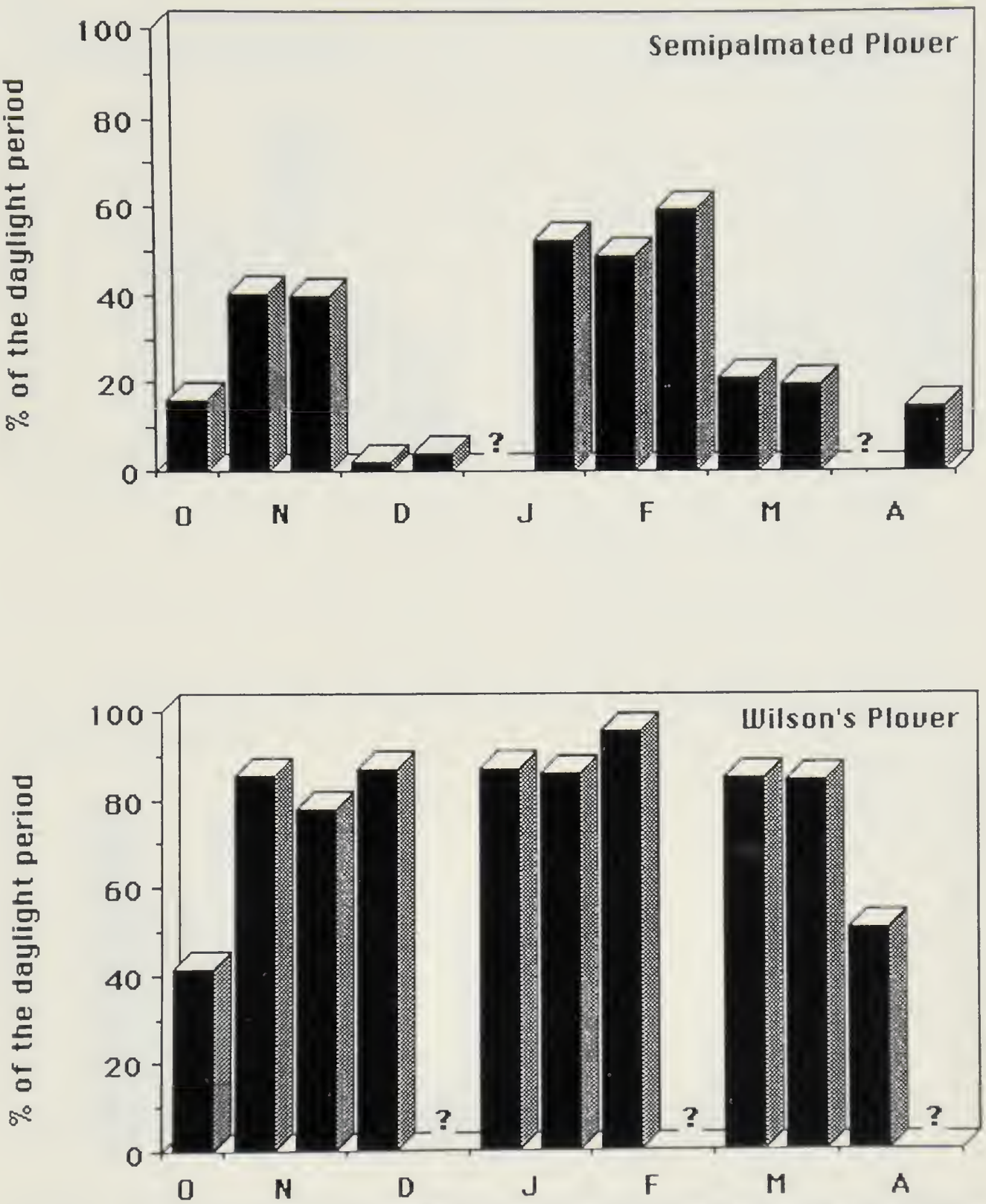

FIG. 2. Seasonal variations in the relative importance of time devoted to resting during the daylight period. Interrogation marks (?) indicate the absence of data.

(Fig. 3). In addition, the increase in aggressiveness in March–April in the former was not observed in the latter.

Semipalmated Plovers preened significantly more on the average (4.9% ± 1.0) than did Wilson's Plovers (1.8% ± 0.5; $t = 4.72$, $P = 0.001$). However, there were no significant seasonal variations in this activity category.

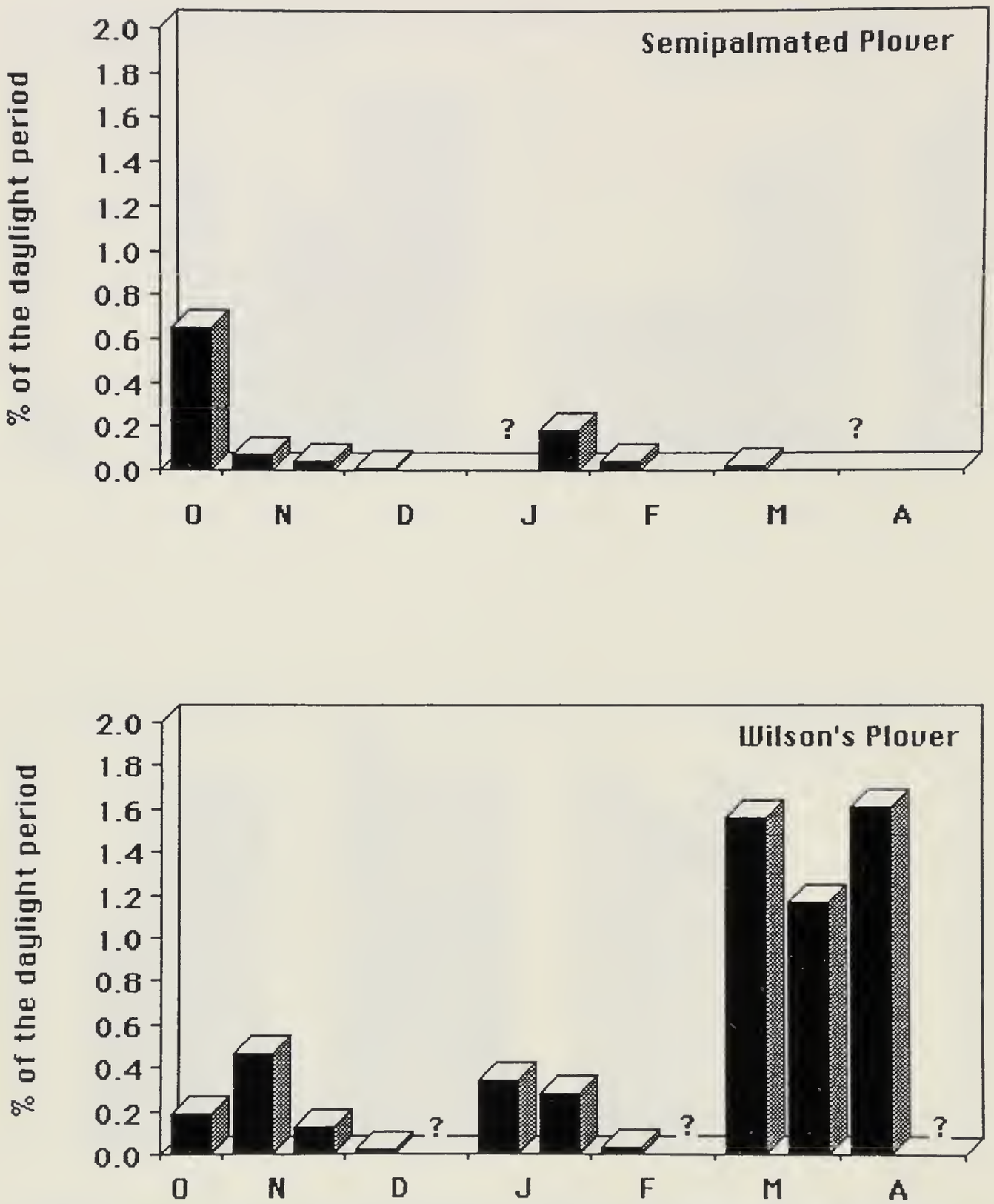

FIG. 3. Seasonal variations in the relative importance of time devoted to aggressiveness during the daylight period. Interrogation marks (?) indicate the absence of data.

The proportion of time spent walking, running, or flying for reasons other than foraging, aggression, or alert was generally low for both species (average = 1.4% ± 0.3 and 1.1% ± 0.5 for Semipalmated and Wilson's plovers, respectively; see Fig. 4). Locomotion in Wilson's Plovers was significantly greater at the end of November and January than in other

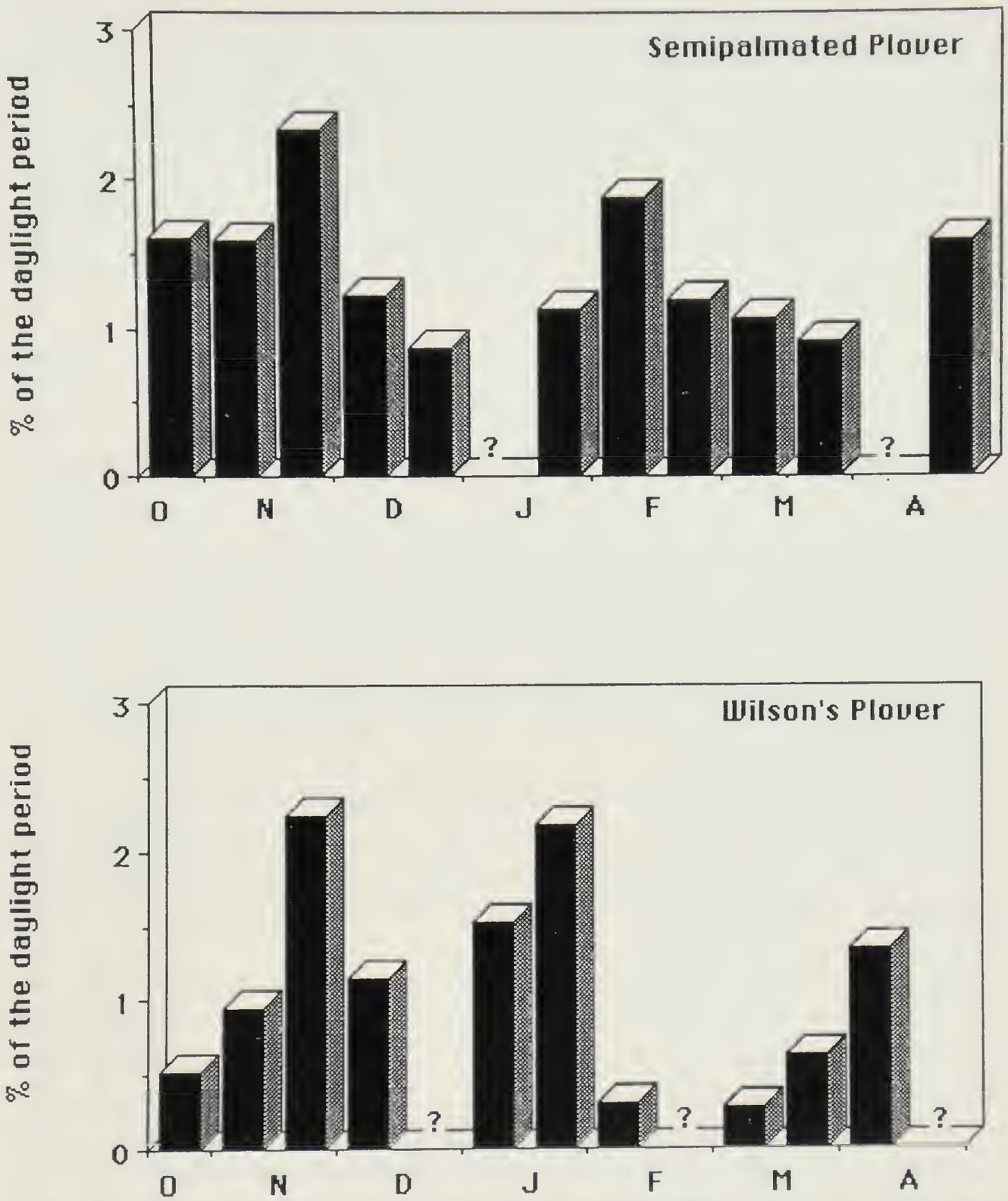

FIG. 4. Seasonal variations in the relative importance of time devoted to locomotion during the daylight period. Interrogation marks (?) indicate the absence of data.

months ($F = 2.17$, $P < 0.05$) but was fairly constant throughout the study period in the other species.

Semipalmated Plovers were alert more often (2.4–7.8%) than Wilson's Plovers (0.9 to 2.8%; $t = 6.64$, $P < 0.001$). However, neither of them showed any significant seasonal variation in alertness.

Daily energy budget of Wilson's Plovers.—Wilson's Plovers principally

ate crabs whose carapace width was equal to a quarter (41.5% of total eaten crabs) or a half (38.6%) of their bill length (Table 4). The estimated number of crabs eaten during the entire daylight period (Table 4) was larger in October, at the beginning of November, and in April (90.1–133.2) than from the end of November to March (1.7–37.3). Their energy content, corrected for $CaCO_3$, averaged 11.37 ± 1.34 J/mg of their dry mass (N = 17). The relationship between the dry mass (W in mg) of crabs and carapace width (C in mm) is: Log W = 3.804 Log C − 4.98 (r^2 = 0.969; N = 207).

The average assimilatable energy in crabs with carapace width equivalent to a quarter, half, and three quarters the bill length was 38.7, 541.4, and 2531.2 J, respectively.

The mean monthly weight of Wilson's Plovers captured in Chacopata Lagoon was constant during the study period, increasing only slightly (insignificant) in April. Similarly, the DEE ranged from 42.6–45.4 kJ between November and March and was only slightly higher at the end of October and at the beginning of April (Fig. 5, Table 5). During daylight, most of the energy was expended while resting, except at the end of October and the beginning of April when more energy was expended in feeding activities (Table 5). Other activity categories resulted in little energy expenditure.

The daylight energy intake of Wilson's Plovers (Table 6, Fig. 5) decreased sharply between the end of October (99.1 kJ) and the beginning of November and even further toward January (2.4 kJ) and the beginning of February (0.04 kJ). Energy intake increased appreciably only at the beginning of April (86.7 kJ).

The daily energy budget (i.e., daily energy intake minus daily energy expenditure) of Wilson's Plovers consequently showed a large deficit from the end of November to the beginning of April (Fig. 5). The balance was positive only at the end of October, at the beginning of November, and at the beginning of April. It must be noted that the energy intake at the beginning of November, large enough to balance the budget, was not due to greater feeding activity (the latter was just about equivalent to that observed at the end of November, beginning of December and March; see Fig. 3) but to greater foraging success (Table 4).

DISCUSSION

Daylight activities of Semipalmated and Wilson's plovers.—Three activity categories attract special attention, i.e., feeding, resting, and agonistic manifestations for which the seasonal patterns of both species greatly differ. In fact, our results largely confirm the predictions concerning the seasonal variations in the proportion of time devoted to energy intake by

TABLE 4

TIME SPENT FORAGING AND NUMBER AND SIZE OF CRABS CAPTURED BY WILSON'S PLOVERS DURING EACH SAMPLING PERIOD

Sampling sessions	T_f[b] (min)	R_f[c]	Carapace width of crabs[a]									Actual total number of captured prey during observations	Estimated total number of captured prey during the daylight period
			¼			½			¾				
			NP[d]	ENP[e]	%[f]	NP	ENP	%	NP	ENP	%		
18–21 October	391.7	0.34	30	54.7	41.1	28	51.1	38.4	15	27.4	20.5	73	133.2
11–12 November	74.5	1.21	17	37.4	41.5	16	35.2	39.0	8	17.6	19.5	41	90.1
21–22 November	106.8	0.19	4	7.4	36.4	4	7.4	36.4	3	5.5	27.3	11	20.3
1 December	69.9	0.27	5	10.5	55.6	3	6.3	33.3	1	2.1	11.1	9	18.9
14–16 January	46.6	0.50	5	9.7	41.7	4	7.8	33.3	3	5.8	25.0	12	23.3
29–30 January	49.1	0.13	1	2.1	33.3	2	4.3	66.7	0	0.0	0.0	3	6.4
15–17 February	13.3	0.13	1	1.7	100.0	0	0.0	0.0	0	0.0	0.0	1	1.7
8–9 March	79.4	0.47	8	15.7	42.1	9	17.7	47.4	2	3.9	10.5	19	37.3
22–24 March	78.8	0.33	7	10.7	41.2	6	9.2	35.3	4	6.1	23.5	17	26.0
11–13 April	315.6	0.36	36	46.0	40.4	34	43.4	38.2	19	24.3	21.3	89	113.6

[a] Carapace width equal to ¼, ½, and ¾ plovers' bill length (average bill length of plovers = 20.5 mm; N = 141).
[b] T_f = total time of daylight spent foraging.
[c] R_f = mean rate of foraging (mean number of prey taken/min).
[d] NP = actual number of prey of that type captured during observations.
[e] ENP = estimated number of prey of that type captured during the complete daylight period.
[f] % = estimated percent of that prey type in the diet.

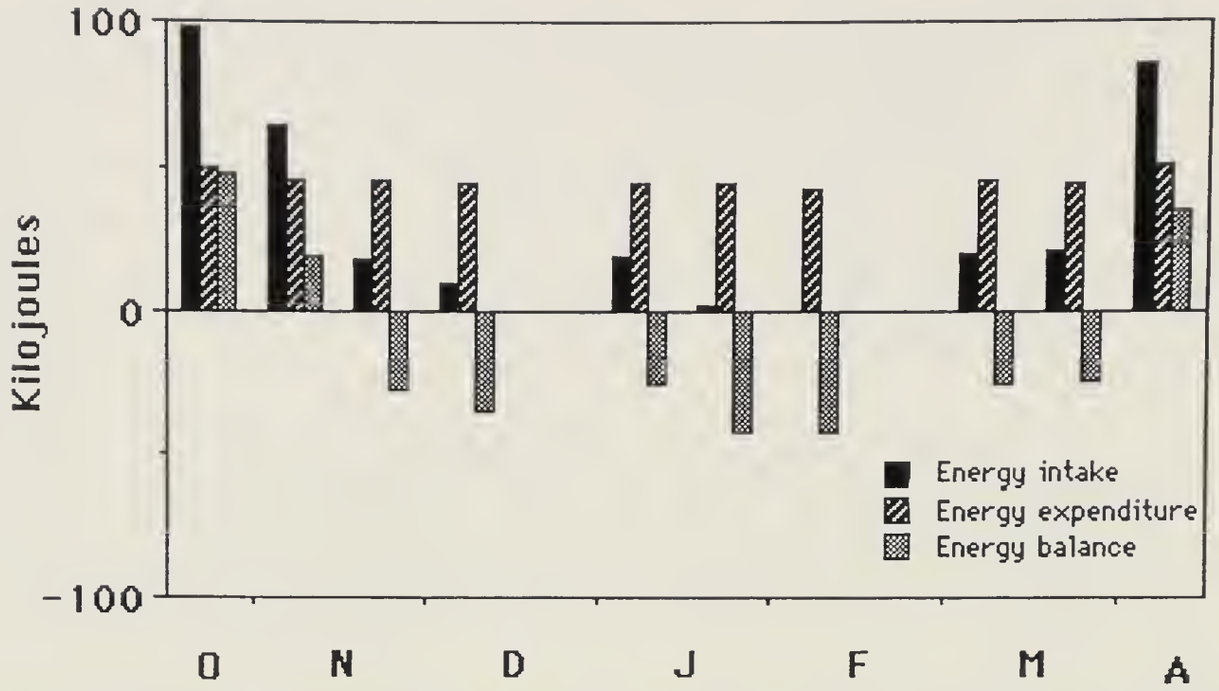

FIG. 5. Seasonal variations in the daily energy budget, on a 24-h basis, of Wilson's Plovers.

migratory and permanent resident shorebirds in the tropics. In addition, in both species, the seasonal resting pattern is typically the reverse of that feeding.

Semipalmated Plovers are present in the lagoons of northeastern Venezuela, including those of Chacopata (Limoges 1987) and Cumaná (McNeil 1970b), especially during fall migration, and between January and April (Limoges 1987). The increase in numbers observed in January suggests regional movements. Semipalmated Plovers undergo their pre-basic molt from August to December (F. Mercier, pers. comm.). The seasonal variations in feeding behavior of the species could be tied to their energetic needs. A certain amount of hyperphagia could take place during pre-basic molt, October–December. Fall-arriving Semipalmated Plovers are likely to be very lean and to devote more time to rebuilding their fat and protein reserves. Plovers devoted more time to feeding in December just before regional movements were observed; however, McNeil (1970a) did not measure the lipid content of the species for the corresponding period. The other period when Semipalmated Plovers devoted more time to foraging corresponds to the pre-migratory hyperphagia which results in the depositing of fat for the northward spring migration. McNeil (1970a) has shown that Semipalmated Plovers, in northeastern Venezuela, have a fat index (% of lean dry weight) averaging 110%, in comparison with values between 15% and 40% in other periods of the year. The species spent less time feeding from January to February, the months when wintering Nearctic shorebird migrants have the lowest fat index. The differences be-

TABLE 5

DAILY ENERGY EXPENDITURE (KJ), ON A 24-H BASIS, OF WILSON'S PLOVER

Sampling sessions	Energy expenditure associated with										Total energy expenditure
	Feeding	Preening	Resting	Flight[a]	Walking	Fight	Ground display	Alert[b]	Running[c]	Nocturnal resting	
18–21 October	18.38	0.58	8.56	0.34	0.12	0.00	0.00	0.62	0.03	21.18	49.81
11–12 November	3.49	0.29	17.44	1.47	0.18	0.00	0.07	0.75	0.12	21.39	45.20
21–22 November	5.01	0.73	15.89	0.67	0.62	0.00	0.02	1.03	0.03	21.42	45.43
1 December	3.28	0.35	17.53	0.02	0.31	0.00	0.00	0.48	0.01	21.72	43.70
14–16 January	2.18	0.86	17.58	0.56	0.35	0.00	0.00	0.80	0.11	21.65	44.08
29–30 January	2.30	0.77	17.50	0.32	0.57	0.00	0.00	1.05	0.09	21.50	44.10
15–17 February	0.39	0.54	19.60	0.00	0.09	0.00	0.00	0.75	0.01	21.26	42.63
8–9 March	3.72	0.24	17.70	0.79	0.06	0.00	0.00	1.46	0.12	20.96	45.06
22–24 March	3.70	0.64	17.81	0.15	0.17	0.06	0.58	0.75	0.04	20.70	44.61
11–13 April	14.83	0.39	10.83	1.02	0.38	0.21	0.03	1.73	0.32	20.43	50.17

[a] Including all flights associated with alert reactions, agonistic manifestations, and locomotion.
[b] Including alert reactions associated with aggressiveness, but excluding flight escape.
[c] Including running for feeding, or ground pursuit and escape.

TABLE 6

CONTRIBUTION OF EACH CLASS OF CRAB SIZE TO THE ESTIMATED TOTAL ENERGY INTAKE (KJ) OF WILSON'S PLOVER DURING THE COMPLETE DAYLIGHT PERIOD

Sampling sessions	Carapace width of crabs[a]			Estimated total daily energy intake
	¼	½	¾	
18–21 October	2.12	27.66	69.28	99.06
11–12 November	1.45	19.03	44.50	64.98
21–22 November	0.29	4.00	14.02	18.30
1 December	0.41	3.41	5.31	9.12
14–16 January	0.38	4.20	14.73	19.31
29–30 January	0.08	2.31	0.00	2.39
15–17 February	0.04	0.00	0.00	0.04
8–9 March	0.61	9.57	9.94	20.12
22–24 March	0.41	4.97	15.50	20.88
11–13 April	1.78	23.49	61.38	86.65

[a] Carapace width equal to ¼, ½ and ¾ plovers' bill length (average bill length = 20.5 mm; N = 141).

tween the January–February and the March–April periods in the proportion of daytime devoted to feeding activities by Semipalmated Plovers are similar to those reported by Zwarts (1990) and Zwarts et al. (1990) for several Palearctic shorebird species wintering in Mauritania.

From November to April, Wilson's Plover devoted much more time to resting than to feeding compared with Semipalmated Plovers. In October (Fig. 1), and also in August and September (B. Gagnon, pers. comm.), the time spent feeding was more than that observed outside the breeding period. The proportion of the day devoted to feeding seemed to vary seasonally with energetic needs. The latter are likely to be higher during the breeding season, which starts in April (McNeil 1970b; B. Limoges, pers. comm.), and during the pre-alternate molt which ends in March–April (F. Mercier, pers. comm.). McNeil (1970b) has shown that Wilson's Plovers of northeastern Venezuela accumulate fat reserves around March–April which average 37% (reaching 54% and 70%) of the lean dry weight. The fat indices of this resident species are by far lower than those observed during the pre-migratory period of Nearctic migrants (e.g., Semipalmated Plovers; see above and McNeil 1970a) but are sufficient to explain the observed increase of time devoted to feeding in March and especially in April.

In Semipalmated Plovers, aggressiveness may occur in migratory stopovers and wintering quarters (Recher and Recher 1969, Doyon and McNeil 1978, Myers et al. 1979, Myers and McCaffery 1984, Myers 1984). However, the species in general showed little aggressiveness during its stay at

Chacopata (Fig. 3). We observed at least two birds defending a feeding territory at Chacopata indicating that such behavior may take place during migrations. This is in accordance with the findings of Recher and Recher (1969), Myers et al. (1979), Myers and McCaffery (1984), and Myers (1984) in a variety of shorebird species including the Semipalmated Plover. Except in March and April, the time devoted to aggressiveness by Wilson's Plovers also was very short. The increase in aggressiveness observed in March and April is correlated with pair formation and breeding territory establishment (Tomkins 1944; Bergstrom 1981, 1988a, b). Strauch and Abele (1979) also concluded that interspecific competition is not very important between Wilson's, Semipalmated, and Collared (*C. collaris*) plovers.

Semipalmated Plovers devoted more time in alert reactions than did Wilson's Plovers, probably because they spent proportionately more time feeding. Wilson's Plovers, motionless and resting during a large part of the daylight period, were well-concealed and thus showed alert reactions less frequently. In contrast, Semipalmated Plovers, devoting proportionately more time to foraging, had to remain more vigilant of predators. In Chacopata, facing a danger from an aerial predator or during alert reactions for unknown reasons, both species adopted very different strategies; Wilson's Plovers crouched or flattened themselves on the ground, while Semipalmated Plovers flew in compact flocks together with small peep sandpipers (*Calidris* spp.).

Daily energy budget of Wilson's Plovers.—The fact that Wilson's Plovers, compared with Semipalmated Plovers, devoted little time to feeding during daylight raises an important question: Can Wilson's Plovers balance their daily energetic needs with so little time passed foraging and so few prey ingested during daylight or do they need to adopt another strategy to fulfill their energetic requirements? Our results do indicate, in fact, that daytime foraging is insufficient, at least from November to April.

In many species of shorebirds of northern regions, daytime foraging seems insufficient for the birds to fulfill their energetic needs during the winter (see Pienkowski et al. 1984). For example, in Britain during midwinter, daylight foraging in Northern Lapwings (*Vanellus vanellus*) provides less than 10% of the birds' existence energy requirements (McLennan 1979). The same may occur in tropical environment (Engelmoer et al. 1984). Insufficiency in daytime energy intake was reported for Bar-tailed Godwits (*Limosa lapponica*) in Mauritania (Engelmoer et al. 1984) and juvenile Curlew Sandpipers oversummering during the boreal summer in South Africa (Puttick 1980). In tropical environments, high daytime temperature and desiccation of the substrate surface may cause prey to come to the surface less frequently (Burger 1984, Batty 1991) and are

likely to be responsible for such a deficit. However, the body mass of Wilson's Plovers at Chacopata did not decrease between the end of November and the beginning of April, even though diurnal foraging appeared insufficient to fulfill their daily energetic requirements. The energy deficit measured in Wilson's Plovers during that period was only apparent.

Two strategies could compensate for a diurnal deficit: the use of accumulated reserves, principally fat, and/or nocturnal feeding.

Many shorebirds wintering in boreal regions accumulate fat reserves to sustain their energetic demands during winter months (Evans and Smith 1975, Davidson 1981, Dugan et al. 1981). A similar phenomenon has also been reported for birds that reside permanently in the tropics, such as Black-necked Stilts which accumulate such reserves "in preparation for the dry season, when food may be relatively scarce for this species" (McNeil 1971). The diurnal energetic deficit observed in Wilson's Plovers is apparently not compensated for by accumulated fat since body mass did not vary seasonally. In addition, Wilson's Plovers collected in other sites close to Chacopata on the northeastern coast of Venezuela maintained, the year round, a very low fat content (18.5–24.7% of the lean dry weight), except just before breeding.

It was shown recently that Wilson's Plovers, as well as Semipalmated Plovers, are active and forage during nighttime at the site of the present study, especially during low tides (McNeil and Robert 1988; Robert and McNeil 1989; Robert et al. 1989; B. Gagnon, pers. comm.). In the daytime, they concentrate their feeding activities during periods of low tide (Strauch and Abele 1979), but do not feed during the totality of these periods in spite of the fact that they do not eat enough to balance their needs. This study shows, however, that they devote proportionately less time to feeding during daylight hours than Semipalmated Plovers and suggests that, at least from November to March, they forage mainly during the night. The time devoted to foraging by Wilson's Plovers during the day was also greatly reduced, in comparison with that of other shorebird species wintering in Arctic (see Puttick 1984), northern temperate (Maron and Myers 1985), southern temperate (Puttick 1979, Hockey 1984), and tropical (Engelmoer et al. 1984, this study) regions.

It thus appears that Wilson's Plovers have a balanced daily energy budget, the birds counterbalancing a diurnal energy deficit by a nocturnal energy intake. However, what are the reasons for a mainly nocturnal foraging strategy?

There are two broad hypotheses, the "preference hypothesis" and the "supplementary hypothesis." The former is that this strategy provides the more profitable or the safer, feeding opportunities; the other is that night feeding occurs only when daytime feeding has been inadequate to meet

the birds' requirements (McNeil, in press). The following arguments give greater support to the "preference hypothesis."

In tropical environments, a decrease in daytime prey availability may result from high temperatures and desiccation of the substratum surface (Burger 1984, Batty 1991). Prey activity, and their availability, may be greater during the night than during daylight (Dugan 1981; Pienkowski 1983a, b; Townshend et al. 1984). Robert et al. (1989) observed this in February at one of the Chacopata foraging sites for many prey types. Their study did not include crabs. In spite of the lack of data comparing diurnal and nocturnal availability and/or accessibility of *Uca* crabs, the preferred prey of Wilson's Plovers, we believe that their nocturnal activity is not due to a daylight food shortage. The Chacopata mudflats are swarming with millions of small crabs, both in the day and at night.

On the other hand, special techniques or strategies could be needed to catch *Uca* crabs: not only do they live in deep burrows out of reach of plovers' bills, but when on the surface, they flee as soon as a bird comes within several meters. According to Zwarts (1985), there is a circle with a radius of 1–3 m around a feeding bird where there are no *Uca tangeri* on the surface (see also Summers 1980). Plovers, by making quick dashes, are able to catch fiddler crabs, but they often pause and wait for the circle devoid of crabs to become smaller as *Uca* reappear on the surface. It is possible that the radius without crabs on the surface around a feeding Wilson's Plover could be smaller during darkness than during daylight. In addition, Zwarts (1990) found that no *Uca* were present at the surface of mudflats when low water occurred in the second half of the night or in the early morning (02:00–08:00 h). At night, the crabs also fed closer to their burrows than during the day (Zwarts 1990). According to Zwarts and Dirksen (1990), *Uca* are very easy to catch in such a situation. Consequently, in the case that *U. thayeri* behave as *U. tangeri,* it would be easy for Wilson's Plovers and other shorebirds to catch them by a wait technique during the first part of the night.

Wilson's Plovers seem better adapted for night feeding than Semipalmated Plovers. Their bill, longer and stronger, is well fitted to catch highly mobile crabs (measuring on the average 7.82 mm) at the surface of the substratum (Strauch and Abele 1979). Semipalmated Plovers are generalist or opportunistic feeders, and have a small bill allowing them to catch varied but smaller prey measuring, on average, 1.81 mm (Strauch and Abele 1979). On intertidal mudflats, their diet largely comprises small polychaeta, buried in the substratum, small insects, crustacea and mollusca (Strauch and Abele 1979, pers. obs.). All these prey types are likely to be less conspicuous at night than the crabs taken by Wilson's Plovers.

The period of low daylight foraging activity of Wilson's Plovers, ex-

cepting April, roughly corresponds to the months when Peregrine Falcons (*Falco peregrinus*) are present over the Chacopata lagoon complex. The latter arrive in November and leave at the end of April (Limoges 1987). The presence of falcons in the lagoon complex could result in some shorebird species not congregating in some areas (e.g., small expanse surrounded by mangroves) during daylight because of possible predation, in spite of their richness in prey organisms. Rather, the shorebirds would exploit them only during darkness (Robert et al. 1989). Limoges (1987) also observed that many of the smaller shorebirds congregate in significantly higher numbers when Peregrine Falcons start chasing them over the Chacopata lagoon. Such a behavior could reduce individual risks of being captured by the aerial predators (Vines 1971, Page and Whitacre 1975). As far as Wilson's Plovers are concerned, gregariousness increased, but not significantly, when the falcons appeared (Limoges 1987). However, compared to Semipalmated Plovers, Wilson's Plovers foraging is dispersed and solitary. According to Limoges (1987), they are more gregarious when roosting than when foraging. Wilson's Plovers could gain more by roosting during daytime, instead of foraging. Being less active, more gregarious, and more concealed, they would be less exposed to predation from Peregrine Falcons or other aerial predators.

Finally, the basal metabolic rate tends to be lower in birds from the tropics compared to birds from colder regions; one explanation for this is that reduced endogenous heat production in the tropics may be advantageous in avoiding heat stress. Since metabolic rates in shorebirds are higher than in other families of birds (Kersten and Piersma 1987), the Chacopata shorebirds may be especially susceptible to warm circumstances. However, our suggestion is that this could apply equally to both species of plovers. There are no data with which to examine whether or not they suffer heat stress, but both species seem to behave differently under the midday sun. On many occasions, Semipalmated Plovers left the mudflats to get shade under mangroves. In contrast, Wilson's Plovers rested in small depressions on the mudflats, apparently seeking protection against midday and afternoon strong winds rather than against full sun (A. Morrier, pers. obs.).

Limits of the method for the daily energy budget.—Kersten and Piersma (1987) present an equation for predicting the basal metabolic rate of shorebirds, derived from data on northern species. Of the several equations used for estimating the basal metabolism of non-passerine birds (see Kendeigh et al. 1977), the equation of Aschoff and Pohl (1970) gives the lowest values, over-estimating the basal metabolism of many tropical species, and under-estimating by 42% that of many shorebirds (see Kersten and Piersma 1987, Mathiu 1989). However, since the present study took place in a tropical environment, the model of Aschoff and Pohl

(1970) is more conservative and likely to be more adequate for Chacopata Wilson's Plovers.

The values for the K-factors allocated to each activity category in calculating the energy expenditure (Table 3) do not result from studies on Wilson's Plovers. Such data are lacking for shorebirds. In the present study, feeding activity, diurnal resting, and the presumed nocturnal resting represent from 92.0 to 97.4% of the total energy expenditure. Other values for the K-factor were used for shorebirds, such as 5.8 (Puttick 1980) and 3.0 (Brunton 1988, Maxson and Oring 1980) for feeding. As did Brunton (1988) and Maxson and Oring (1980), we used a K-factor equal to 1.24 both for diurnal and nocturnal rest. Puttick (1980) used a K-factor equal to 1.35 for diurnal rest.

Our values for energy expenditure thus seem under-estimated for many reasons. First, as mentioned above, it has been shown that Wilson's Plovers are active and feed during nighttime at the site of the present study. Nocturnal activities are particularly important from November to March. The cost of such activities was not included in our estimates, because we presupposed that Wilson's Plovers were resting from dusk to dawn. In addition, Wilson's Plovers suffer their pre-alternate molt from February to April (McNeil 1970b; F. Mercier, pers. comm.). Pre-basic molt takes place in August and September (F. Mercier, pers. comm.), but may extend up to December (McNeil 1970b). The energetic cost of molting and thermoregulation also were not considered here.

The actual energy intake, on the other hand, is likely to have been over-estimated. In the present study, except during mid-winter, crabs whose carapace width was equal to three quarters of the length of the plovers's bills counted for 10–20% of their diet and for 49–76% of their total energy intake. The relationship between the energy content of crabs and their size is exponential, and a slight over-estimation of the latter would suffice to over-estimate energy intake appreciably. In Panama, Wilson's Plovers were found to have about the same diet (96% crustacea) as at Chacopata, but the maximal width of ingested crabs was equal to 10 mm. Crabs equal in size to three-quarters the bill length of plovers are likely too big to be swallowed. It is quite possible that we sometimes over-estimated the size of crabs, especially because of the difficulty in visualizing the carapace without including the legs.

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MIGRATION AND MASS CHANGE OF WHITE-RUMPED SANDPIPERS IN NORTH AND SOUTH AMERICA

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Abstract.—White-rumped Sandpipers (*Calidris fuscicollis*) migrate between Canadian Arctic breeding areas and "wintering" areas in Patagonia, one of the longest animal migrations in the Western Hemisphere. Migrant White-rumped Sandpipers employ both long-distance, nonstop, and short-distance multiple-stop flights. Southbound migrants fly over the Atlantic ocean from northeastern North America to South America. They then gradually move southeast along northeastern coasts before turning inland in trans-Amazonian travel requiring about one month. Northward migration routes from Patagonia evidently are similar, but are traversed in a rapid series of long nonstop flights. Staging zones are unknown in northern South America during north migration, in the Caribbean basin, or on the Atlantic coastal plain of the U.S. A major staging area is identified in the Great Plains, where birds evidently prepare for a last remaining flight to the Arctic. The migration system of this small sandpiper makes the species vulnerable to loss of strategic migration habitats. *Received 11 Dec. 1990, accepted 10 April 1991.*

Studies of avian migration energetics generally have focused on migration before long flights over ecological barriers such as oceans or deserts. There are few studies of energetics in the context of an annual migration strategy, especially in the case of trans-hemispheric migrants. The present study focuses on long-distance migration in the context of a full annual cycle.

The White-rumped Sandpiper (*Calidris fuscicollis*) is one of the longest distance bird migrants in the Western Hemisphere. Studies of its southward migration (McNeil and Cadieux 1972a; McNeil and Burton 1973, 1977; Burton and McNeil 1975) have confirmed long distance, transoceanic routes between eastern Canada and northeastern South America, as first postulated by Cooke (1910). Relatively little is known about how the remaining migration is completed between Canadian Arctic breeding areas and austral wintering latitudes of South America. This paper gives an annual perspective of distribution, use of migration staging areas, timing, and mass change during north and south migrations.

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The energetics of long flights have been investigated by Odum (1958) and others, studying passerine migrants, and by McNeil (1970), McNeil and Cadieux (1972a), Davidson (1984), and Castro and Myers (1988, 1989), studying shorebirds. These studies found that birds accumulate fat which is later metabolized to fuel long, over-water flights. Methods were developed for estimating flight-distance capacities based on the amounts of fat birds had accumulated. More recent studies (e.g., Davidson and Evans 1988) suggest that metabolism of muscle protein may also contribute a small amount to migration energy requirements. We provide data on fluctuations in the mass of White-rumped Sandpipers during migration and winter and use formulae (McNeil and Cadieux 1972b, Castro and Myers 1988) to estimate flight-distance capabilities at different seasons. We combine this information with observations of seasonal distribution to provide an integrated picture of this small sandpiper's hemispheric migration strategy.

METHODS

White-rumped Sandpipers from different locations and years in both North and South America (Table 1) provide data for this study. All birds were captured either with mist nets or walk-in traps and later released or were collected under permit (McNeil 1970). Mass to the nearest gram was measured with Pesola spring scales or with an Ohaus balance. Although we assume that the masses we recorded are representative of each locality, we cannot assess this as data were not available over a series of years. Where listed in text, mean values are given with ± one standard deviation.

Wing lengths usually were measured by flattening and straightening the primaries before measuring. However, Harrington measured unflattened wing chord lengths. These have been adjusted by adding 3 mm to measurements, this value being intermediate to those used for similar adjustments applied to Dunlin (*Calidris alpina,* 4 mm, Pienkowski et al. 1979) and Semipalmated Sandpipers (*Calidris pusilla,* 2.6 mm, Harrington and Morrison 1979).

Flight ranges (FR) were calculated using the formula of McNeil and Cadieux (1972b) as follows:

$$\text{Flight Range} = \frac{[\text{FW} - \text{Y}] \times \text{S} \times 9.1 \text{ kcal}}{\text{Antilog}(\log 37.151 + 0.744 \times \log \text{W}),}$$

where FW = total mass in grams, S = flight speed (km/h) for the species (80 km/h for White-rumped Sandpipers), W = total mass in kg, Y = 6.44 + 2.55 (wing length in cm, adults and immatures) or Y = 5.66 + 2.63 (wing length in cm, adults only). Flight range capacity was calculated for each locality based on the mean of the ten highest FR values. We assume that the ten highest values represent birds having attained departure mass, but cannot test this assumption. We also expect that some individuals leave at lower fat levels as appears true in other sandpipers (Dunn et al. 1988). The FR's of Magdalen Island birds and a few from coastal Venezuela were calculated using data from fat extraction (McNeil and Cadieux 1972a, b), but substituting the value of 9.5 with 9.1 kcal/g of fat (Johnston 1970, Blem 1990) to be consistent with the above formula.

Regression analysis was used to determine whether body size (as indicated by wing length) influenced the regression of mass or FR values against date. Mass change through time is

TABLE 1
NAMES AND LOCATIONS OF SITES USED IN THIS REPORT

Site name	Location	Years	Source
Magdalen Islands, Quebec, Canada	47°30′N; 61°50′W	1969, 1971	McNeil
Venezuela (coast)	10°25′N; 63°50′W	1966–1967, 1984–1986	McNeil
Venezuela (inland)	8°31′N; 67°35′W	1982–1984	Thomas
Suriname (coast)	5°55′N; 54°55′W	1975, 1978, 1980	Spaans
S. Brazil, Lagoa do Peixe	31°20′S; 51°00′W	1984	Harrington
		1986–1987	Resende and Leeuwenberg
Kansas	38°30′N; 99°05′W	1978, 1985, 1987	Martinez

depicted by linear regression of mass against date. Weight change was not determined for individual birds due to low numbers of recaptures.

During northward migration in 1989 and 1990, Castro measured fat levels of 21 White-rumped Sandpipers at Cheyenne Bottoms, Kansas (Castro 1990). Using this same sample as a basis for comparing flight distance capacity, as estimated by two different formulae, we determined fat content, following the methods of McNeil and Cadieux (1972b), and compared the results to Castro's measured fat levels (Castro, unpubl. data).

We also estimated how many hours White-rumped Sandpipers could fly by first calculating fat-free, wet mass of individuals using the formula of McNeil and Cadieux (1972b), and then subtracting this value from the known mass to estimate the amount of fat. This was converted to kilojoules (kJ) assuming 39.5 kJ/g of fat (Blem 1990). Then we estimated hourly energy expenditure in kJ according to formula *b* of Castro and Myers (1988). We used the latter values for estimating the time the available fat could fuel flight. The maximum ten values at each site were used for comparisons among sites.

We used molt terminology of Humphrey and Parkes (1957). Statistical tests of mass differences between sites were by analysis of variance. Rates of mass change between sites were compared by linear regression of mass against date and then testing for heterogeneity between the slopes (SAS GLM procedure; SAS 1985, 1986).

RESULTS

Flight range estimates.—The McNeil and Cadieux (1972b) formula consistently overestimated ($\bar{x} = 9.47 \pm 1.69$ g, N = 21) Castro's measured lean mass levels at Cheyenne Bottoms. We have no way to resolve which values were correct. Differences of estimates by the two methods were lowest in heaviest birds. Because our study focuses on heaviest birds, the difference between the methods is not important to our evaluations.

Southward migration, Magdalen Islands, Canada.—Adult White-rumped Sandpipers arrived principally during August and early September. Few were caught after 11 September, presumably because most had migrated. At about this same time, increasing numbers of juveniles began

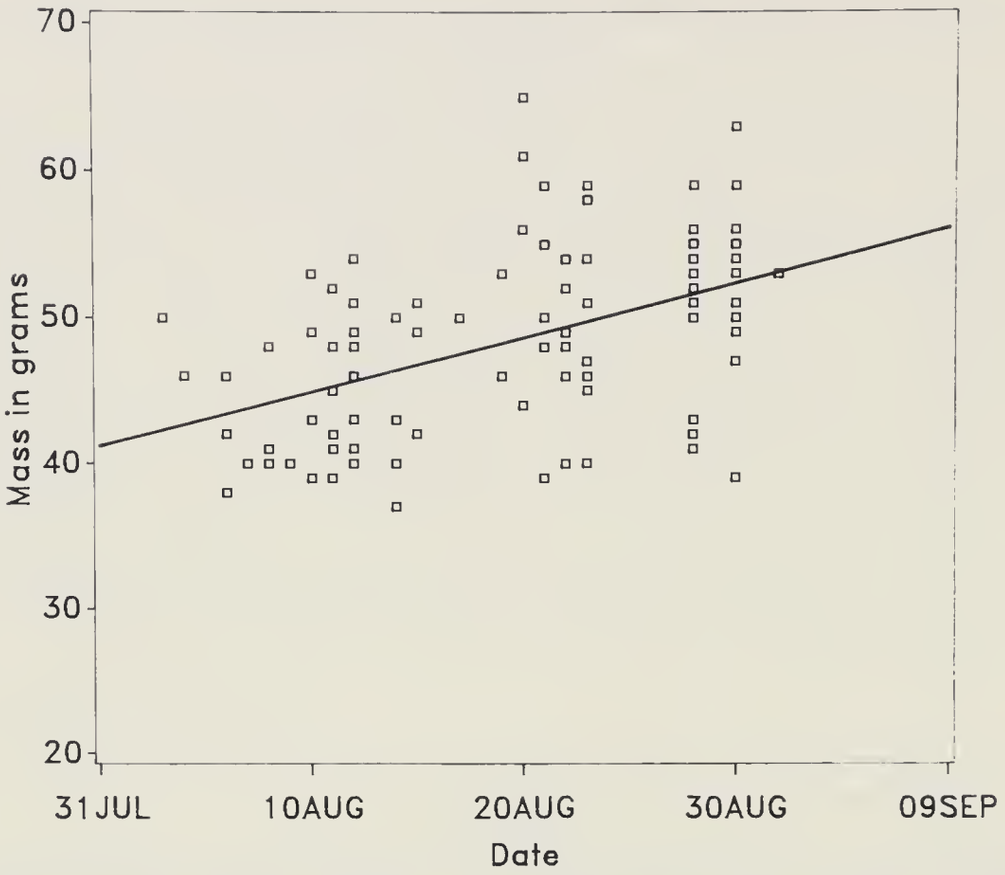

FIG. 1. Regression plot of adult White-rumped Sandpiper mass during August at the Magdalen Islands southern migration staging area in Quebec, Canada. The regression line formula is $Y = 2.15 + 0.20X$, $P < 0.001$.

to be captured. Weekly average mass of adults increased steadily (0.2 g/day, Fig. 1) between mid-August and mid-September. Average mass of juveniles increased steadily between mid-September and early November. Adults and juveniles gained mass at similar rates, as indicated by similar regression line slopes ($P = 0.895$).

We did not find differences of wing lengths among adult birds caught on different dates ($R = 0.014$, $P = 0.893$). We found no primary feather molt nor any significant correlation between mass and wing length ($R = 0.033$, $P = 0.77$). Therefore, we conclude that the relationship ($R = 0.461$, $P < 0.0001$) between date and mass increase was caused by increased mass through accumulation of fat and protein (Davidson and Evans 1988, McNeil and Cadieux 1972a), rather than by some other factor such as arrival and departure of different sized birds.

The ten highest flight range capacity (FR) values of White-rumped Sandpipers in the Magdalen Islands (Table 2) ranged from 3200 to 4050 km for adults and from 3450 to 4150 for juveniles. Mean values of the two age groups did not differ significantly ($P > 0.05$). Energy expenditure estimates (Castro and Myers 1988) suggest that the heaviest individuals were capable of sustaining flight for 40–45 h (Table 3), assuming that only lipids are metabolized. This translates to distance estimates of 3200–3600

TABLE 2

TEN HIGHEST FLIGHT RANGE (FR) ESTIMATES OF WHITE-RUMPED SANDPIPERS DURING SOUTHWARD MIGRATION, ROUNDED TO NEAREST 50 KM

Place	Magdalen Islands[a]		Venezuela coast[b]	Suriname coast	L. do Peixe Brazil
N	30 (Juveniles)	56 (Adults)	18	28	24
Period	7 Oct–5 Nov	20 Aug–6 Sep	1 Aug–3 Nov	20 Aug–20 Sep	29 Oct–21 Nov
	4150	4050	1950	1900	2400
	4100	3800	1250	950	2100
	4100	3700	450	400	1800
	4000	3650	400	100	1350
	3900	3600	300	100	1150
	3700	3550	250	0	850
	3600	3550	100	0	850
	3550	3250	0	0	750
	3500	3250	0	0	650
	3450	3200	0	0	650

[a] FR estimate based on extraction from collected birds.
[b] Flight range estimate based on fat extraction on collected birds; otherwise values were calculated using formulae of McNeil and Cadieux (1972b) on live birds.

km which is very similar to the estimates derived from the FR values, assuming an 80 km/h flight speed.

Northeastern South America.—White-rumped Sandpipers pass through Suriname between mid-August and late September (Spaans 1978). Mean mass of adults was not different between Suriname and Venezuela (ANOVA, $P = 0.3633$) but was substantially lower than at the Magdalen Islands, Canada (ANOVA, $P < 0.01$). We did not have enough juveniles for

TABLE 3

ESTIMATED POTENTIAL DURATION OF FLIGHT[a] FOR WHITE-RUMPED SANDPIPERS AT DIFFERENT LOCATIONS DURING MIGRATION

	Southward migration period			Northward migration period		
	Quebec, Canada	Venezuela	Suriname	Southern Brazil	Venezuela	Kansas
Hours (mean)[a]	43.14	0.05	4.73	41.31	9.80	40.02
SD	2.07	0.16	8.45	1.52	9.00	1.17

[a] Based on the ten highest individual estimates for each location, using fat data of Table 2 and an hourly colloidal fat metabolism rate derived from Castro and Myers (1988).

comparison. Only three of the 46 White-rumped Sandpipers in Suriname/Venezuela had FR values greater than 1000 km (Table 2), and there was no correlation between mass increase and advancing date ($r^2 = 0.03$, $P = 0.25$; Table 2).

Southern South America.—Small numbers of White-rumped Sandpipers begin arriving in southern Brazil about two weeks after the main departure from the Guianas. At Lagoa do Peixe, numbers increase gradually in September and October and sharply between mid-November and December (Resende 1988). The same pattern was observed on the mid-Atlantic coast of Argentina (International Shorebird Surveys, unpubl. data).

Average mass and FR index values at Lagoa do Peixe, first measured a number of weeks after some White-rumped Sandpipers had been present, were higher than values from Venezuela and Suriname (Tables 2, 3). This suggests that some were capable of further southward migration and/or that they retained substantial reserves following flights from northeastern South America.

Austral summering period.—White-rumped Sandpipers are found commonly in southern Brazil between October and May (Belton 1984, Harrington et al. 1986, Resende 1988). Mass ($\bar{x} = 37.2 \pm 4.5$ g, N = 297) remained relatively low and stable during the austral summer. However, for unidentified reasons, during the first 15 days of February 1987, average mass was substantially lower ($\bar{x} = 32.4 \pm 3.3$ g, N = 39, $P < 0.001$) than in other 15-day periods.

White-rumped Sandpipers finish pre-basic molt soon after returning to austral latitudes. The pre-alternate molt of many birds is virtually completed by mid-March (Resende 1988) before northward migration begins. We evaluated whether there were differences of mass at different stages of the molt but found no significant trends. No explainable patterns of mass change were identified until mid-April, when White-rumped Sandpipers began premigratory fattening (see below).

Northward migration, southern South America.—At Peninsula Valdez, Argentina, numbers of White-rumped Sandpipers begin gradually declining in late February (International Shorebird Surveys, unpubl. data). In 1980, numbers declined sharply during late March but remained high until 5 April in 1981 (International Shorebird Surveys, unpubl. data).

In southern Brazil, numbers of White-rumped Sandpipers declined gradually during February 1988 and more sharply during March (Resende and Leeuwenberg, unpubl. data). During an unusual drought in 1989, when Lagoa do Peixe dried almost completely, White-rumped Sandpipers departed in early January (Resende and Leeuwenberg, unpubl. data).

No substantive change of mass occurred in White-rumped Sandpiper

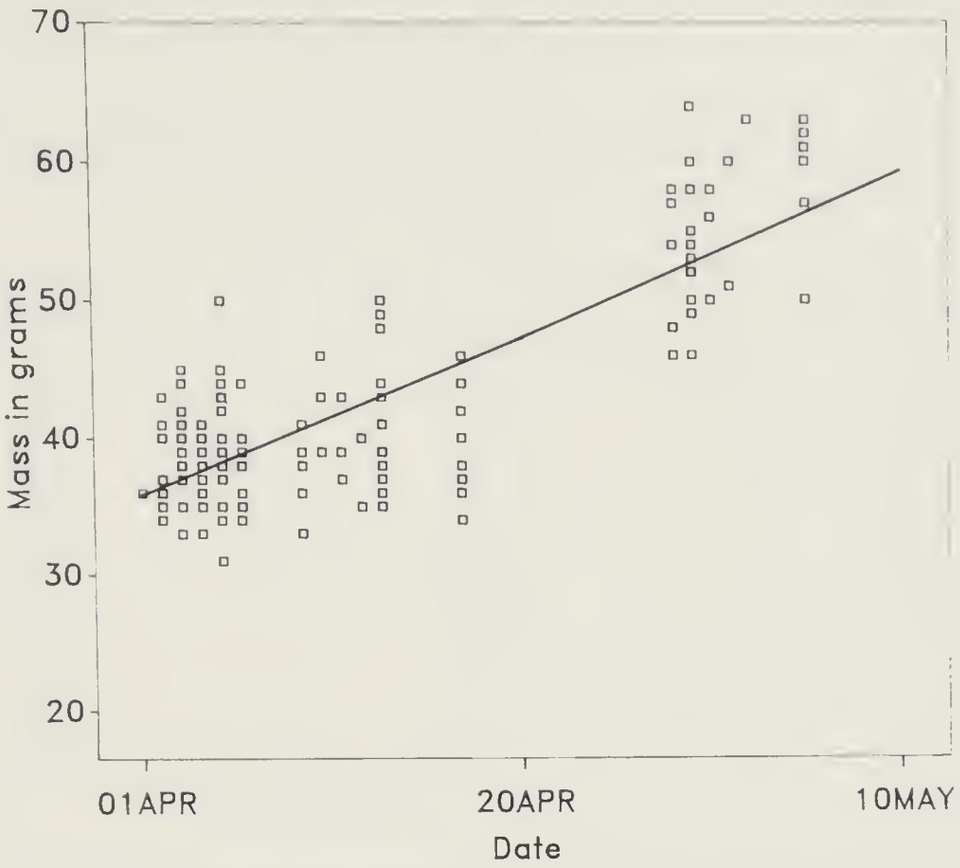

FIG. 2. Regression plot of adult White-rumped Sandpiper mass between 1 April and 5 May at the Lagoa do Peixe migration staging area, Rio Grande do Sul, Brazil. The regression line formula is $Y = -18.81 + 0.60X$, $P < 0.001$.

during two seasons at Lagoa do Peixe before mid-April (Resende 1988, Harrington et al. 1986). Mean mass then increased sharply ($R = 0.85$, $P < 0.0001$; Fig. 2) during late April and early May 1984. Frequent resightings of marked individuals and the steadily increasing average mass (Fig. 2) indicate that the lagoon was being used as a pre-migration staging area (Harrington et al. 1986). This pattern was not seen during the 1989 drought.

Northern South America and the U.S.—The principal northward migration of White-rumped Sandpipers in Venezuela and Suriname is between late April and mid-May (McNeil 1970, Spaans 1978, Thomas 1987). Individuals caught in Venezuela between early April and early June ($\bar{x} = 35.1 \pm 4.00$ g, N = 203) were substantially lighter than those caught during April/May in Brazil ($\bar{x} = 55.9 \pm 5.27$ g, N = 39), and their FR values (Table 4) were consequently much lower. At both the inland and coastal sites in Venezuela, there was no consistent mass increase with advancing date ($P = 0.794$ inland; $P = 0.859$ coastal).

In contrast to Venezuela, numbers of White-rumped Sandpipers at Cheyenne Bottoms, Kansas, gradually increased between late April and late May (Fig. 3). Maximum counts during seven years generally were

TABLE 4

TEN HIGHEST FLIGHT RANGE (FR) ESTIMATES[a] (ROUNDED TO NEAREST 50 KM) OF WHITE-RUMPED SANDPIPERS BASED ON MASS DURING THE NORTHWARD MIGRATION

Place		
Cheyenne Bottoms 12 May–2 June	Venezuela coast 20 Apr–1 June	So. Brazil 13 Apr–4 May
3750	1900*	4600
3650	1800*	4200
3650	1650	4200
3650	1550	4000
3550	1500*	4000
3450	1500*	3950
3350	1450*	3750
3350	1250*	3750
3350	1250*	3750
3250	1250*	3550

[a] Estimates calculated according to McNeil and Cadieux (1972b) except as indicated.
* FR estimate based on fat extraction from collected birds.

during the last ten days of May (Fig. 3), about ten days after the peak in Venezuela (McNeil 1970, Thomas 1987). The Kansas peak is later than the peak of much lower numbers near Decatur, Alabama, where D. Hulse censused shorebirds for eight years for the International Shorebird Surveys (Fig. 3).

The buildup of White-rumped Sandpiper numbers at Cheyenne Bottoms during late May suggests immigration with little emigration of migrants before a threshold date, a pattern characteristic of migration staging areas used for fattening. Therefore, it is no surprise that average mass increased steadily and markedly (Fig. 4, $P < 0.001$), resulting in high FR capacities (Table 4).

DISCUSSION

Southward migration.—White-rumped Sandpiper southward migration happens later than for many congeners. In the Bay of Fundy, Canada, numbers do not increase appreciably until mid-August, after the peak of Semipalmated (*C. pusilla*) and Least (*C. minutilla*) sandpiper migration is past (Hicklin 1987). The species is less common in New Brunswick and Nova Scotia (Hicklin 1987, Maritimes Shorebird Survey, unpubl. data) than farther north and east (Todd 1963, Morrison 1984). Studies at the Magdalen Islands and at Sable Island (McNeil and Cadieux 1972a, McNeil and Burton 1973, Burton and McNeil 1975, this study) show that White-

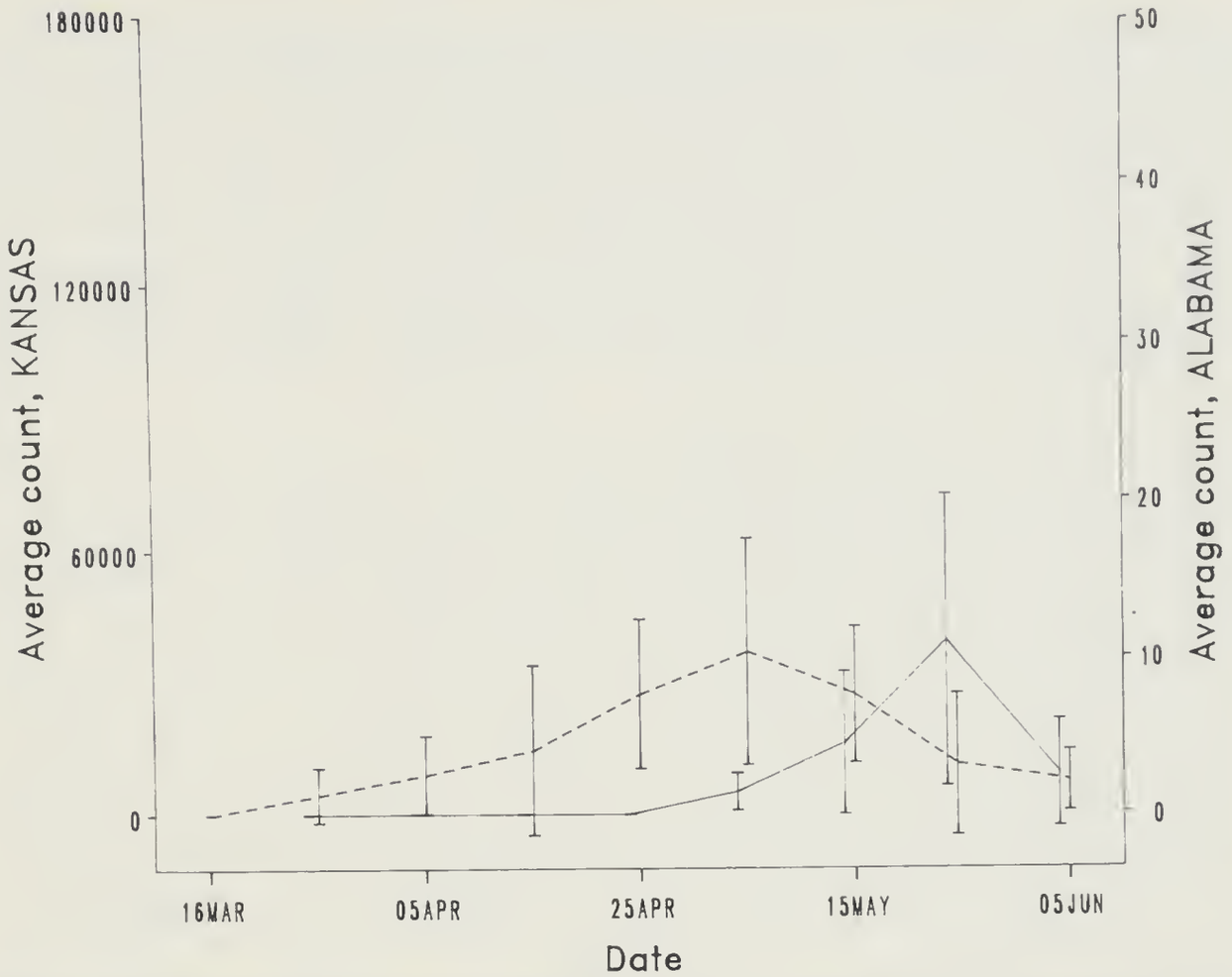

FIG. 3. Average counts (±1 SE) of White-rumped Sandpipers per 10-day period during northward migration at Cheyenne Bottoms, Kansas (left scale, solid line) and at Decatur, Alabama (right scale, broken line) based on five or more years of censusing at each site. Data are from the International Shorebird Surveys.

rumped Sandpipers fly directly over the Atlantic Ocean from eastern Canada to northeastern South America. They arrive principally in the Guianas during late August, where they remain through mid-September (Spaans 1978).

Ours and earlier work (see below) show that White-rumped Sandpipers employ low altitude, "short-hop" flights during the next migration stage along the Guyana and Suriname coasts (Spaans 1978). This is in accordance with our low flight range (FR) index (Table 2); few birds were capable of flying more than a few hundred kilometers without stopping. Coastwise migration probably continues along the northwest Brazilian coast to areas east of the Amazon River mouth (Antas 1983).

The next portion of southward migration is not well known. Antas (1983) indicates there is an overland trip between northern and southern Brazil, with short flights and frequent stops on river bars and banks during September/November when water levels are low. Our summary for the timing of this leg of the migration (about a month) supports the Antas

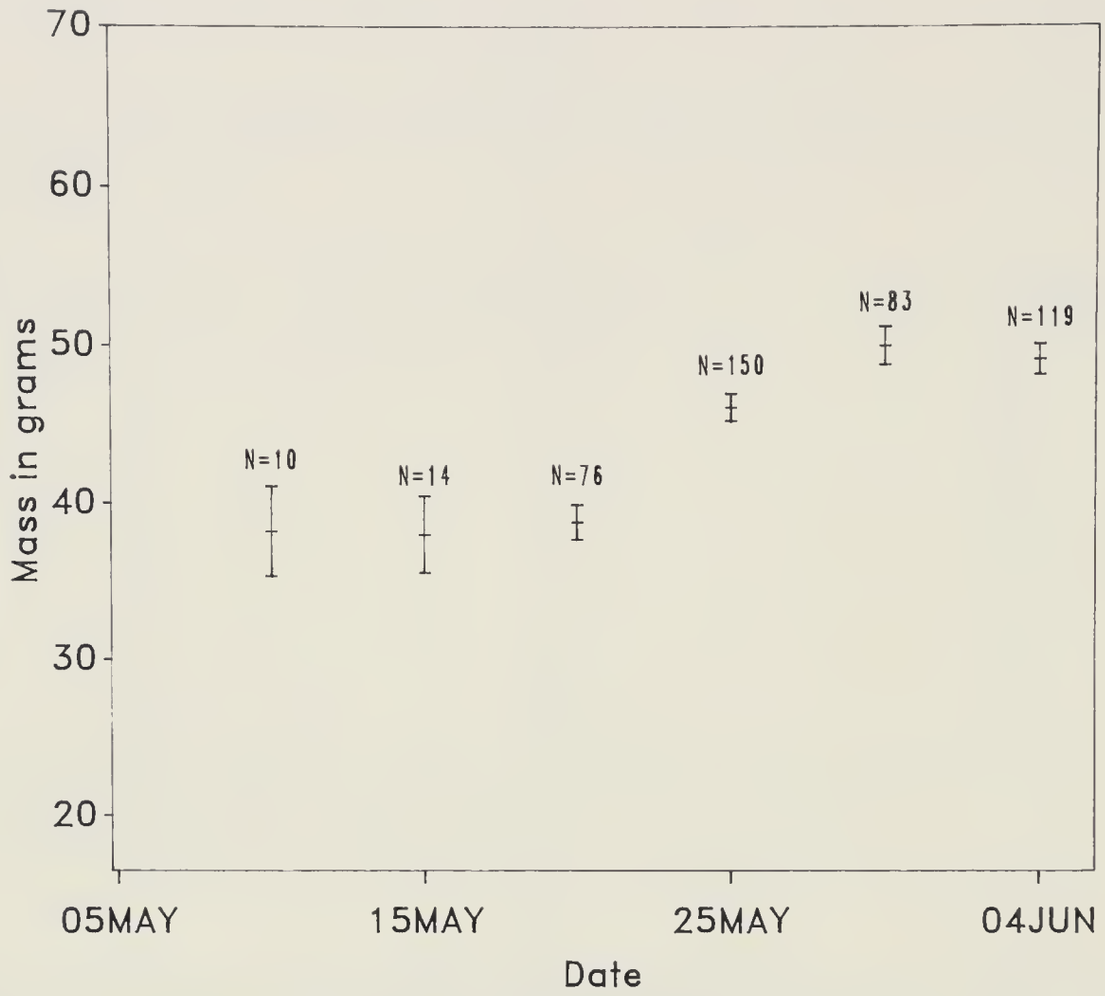

FIG. 4. Average mass per 5-day block of White-rumped Sandpipers (±1 SE) at Cheyenne Bottoms, Kansas, 1 May–4 June, based on data from 450 birds captured for banding during three years.

hypothesis. The alternative possibility, a coastwise migration around eastern Brazil, is not supported by data from routine censuses of suitable coastal habitat near Recife, one of the easternmost points of Brazil, where the species is rare (Severino de A. Júnior, in litt.).

Wetmore (1927) observed White-rumped Sandpipers in Paraguay on 6 September, about the same time as first arrivals in southern Brazil (Belton 1984). Numbers at Lagoa do Peixe, Rio Grande do Sul, increased rapidly between mid- and late-October (this study). Although some individuals remained there through the austral summer (Resende and Leeuwenberg 1987, Resende 1988), the principal "wintering" area is in southern Argentina and Chile (Wetmore 1927). First arrivals appear at Peninsula Valdez, on the central Atlantic coast of Argentina (latitude 42°S) during mid-September; numbers continue increasing through October and November (International Shorebird Surveys, unpubl. data). In Tierra del Fuego, numbers also begin increasing during September (Humphrey et al. 1970).

Northward migration.—Early northward White-rumped Sandpiper migration is not conspicuous. At Peninsula Valdez, departures evidently began in late March (International Shorebird Surveys, unpubl. data); in 1981 we recorded sharply reduced numbers during the first ten days of April. Myers and Myers (1979) noted departure from drying habitats in Buenos Aires Province (latitude 37°S) during late March and early April but not until early May in suitable wet habitats. Wetmore (1927) reported northward migration during early March in western Buenos Aires Province.

Antas (1983) notes the northward migration of White-rumped Sandpipers in Brazil happens when water levels of rivers are high. He concludes that birds must either follow a long coastal route, or use non-stop flights to traverse a shorter, overland route between southern and northern South American coasts. The latter possibility would require large fat deposits. During our work in 1984, we found exceptionally heavy individuals in southern Brazil during late April/early May. This was followed by an exodus of migrants between 1–8 May (Harrington et al. 1986). Our FR estimates argue that nonstop flights to the north coast were possible. If our flight speed estimate of 80 km/h is low (see McCabe 1942), then the flight distance capacity would be greater.

In northeastern Venezuela, numbers of White-rumped Sandpipers during northward migration are five times higher than during southward migration (McNeil 1970). This pattern is reversed farther east, in Suriname, where Spaans (1978) found lower numbers in April–May as compared to September (Spaans 1978).

In the llanos of Venezuela, far from the coast, there apparently were two migration "waves" in 1984, one 26 April–4 May, and another 13–16 May (Thomas 1987). The variability of routine counts, and the low masses of White-rumped Sandpipers in the Venezuelan llanos (Thomas 1987), indicate high turnover rates.

At a coastal site in eastern Venezuela, Francine Mercier's weekly counts (unpubl. data) showed fluctuating numbers between mid-April and late May. There was no gradual buildup characteristic of migration staging sites. The low FR values from the Venezuela coast also did not indicate staging behavior. In short, we found no direct evidence of staging for nonstop flights to the United States. Nevertheless, comparison of migration dates in Venezuela and Kansas (see below) suggest a rapid passage. In addition, three individuals marked by Thomas in Venezuela between 25 April and 14 May were seen in Texas and Kansas between 14 and 23 May.

Distributional evidence also suggests a nonstop flight from South Amer-

ica to North America. The White-rumped Sandpiper is rare in Colombia (Remsen 1977), in Central America (Ridgley 1976, Slud 1964), and on Caribbean Islands (Raffaele 1989; International Shorebird Surveys, unpubl. data). It also is unusual in peninsular Florida and on the U.S. Atlantic coast during spring (Longstreet 1934; International Shorebird Surveys, unpubl. data). Peak but low numbers farther west, in Alabama (Fig. 3), occur at about the same time as peak numbers in Venezuela (McNeil 1970, Thomas 1987) but considerably earlier than peak numbers in the Great Plains (see below).

The principal northward migration of White-rumped Sandpipers in North America is through the Great Plains (Bent 1927). The species is scarce in the east, for example Delaware Bay (Dunne et al. 1983), New England (Forbush 1925), James Bay (Harrington, unpubl. data), and the Canadian Maritimes (Hicklin 1987). Although seen regularly in southern Canadian prairies between late May and mid-June (Colwell et al. 1988), the timing and low numbers suggest "fallout" from an overhead migration rather than buildup characteristic of staging areas. Farther north and west, for example near Edmonton, Alberta, White-rumped Sandpipers are rare in spring (Sadler and Myres 1976).

The increasing numbers and masses of White-rumped Sandpipers in Kansas during May and early June (Fig. 3, 4) indicate a major staging zone where birds obtain sufficient fat to fuel non-stop flights to central Arctic Canadian breeding areas. According to unpublished data in the International Shorebird Survey, more White-rumped Sandpipers can sometimes be found at Cheyenne Bottoms in Kansas than from the combined spring counts at more than 300 other locations that were censused at the same time. White-rumped Sandpipers typically arrive in breeding areas between late May and mid-June (Parmelee et al. 1968), very soon after numbers decline in the Great Plains (Fig. 3).

Comparison of mass gain rates in northward and southward migration.—Our data show variable patterns of mass gain by White-rumped Sandpipers during migration. In some cases, the patterns appear related to whether samples are from staging sites where individuals remain for days and add fat, for example the Magdalen Islands, Lagoa do Peixe, or Cheyenne Bottoms, or whether they are from areas where individuals visit briefly. Examples of the latter are the Venezuela and Suriname sites which were characterized by fluctuating numbers of White-rumped Sandpipers (Thomas 1987; Francine Mercier, unpubl. data) and by low masses (see above).

Seasonal differences in rates of mass increase at major staging sites also exist. We compared rates of mass gain at the three staging sites by charting daily averages against time. To ensure comparability, we restricted eval-

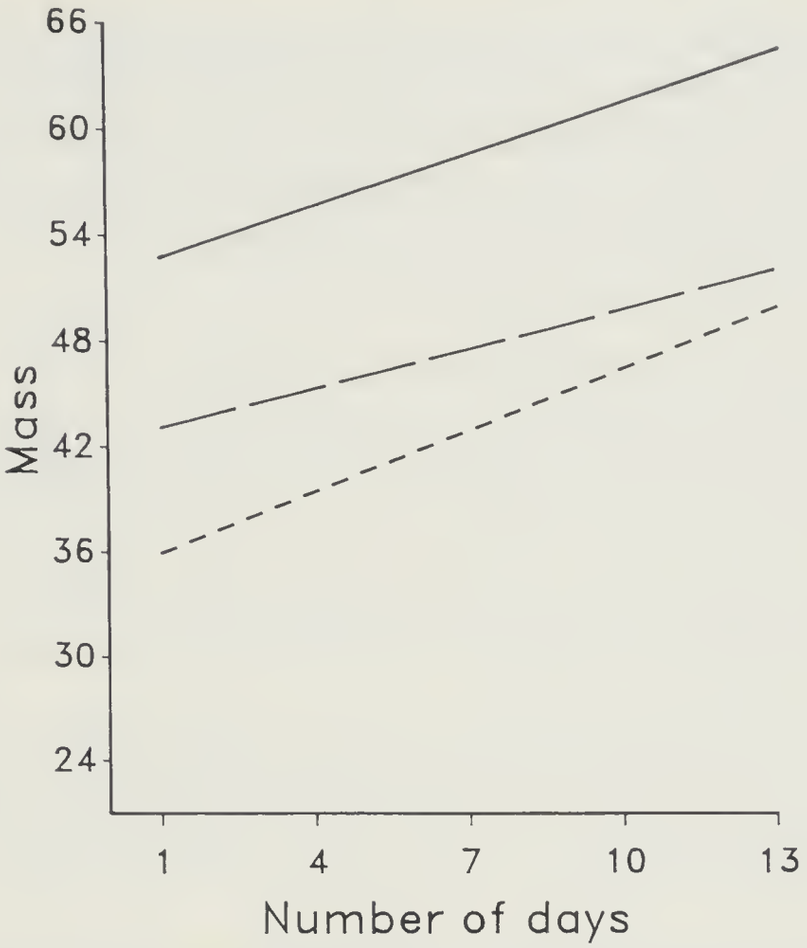

FIG. 5. Rates of White-rumped Sandpiper mass gain during 15 days of the maximum mass-gain period at three widely separated migration staging areas in North and South America, including southern Brazil during April–May (solid line), Kansas in the United States during May (dotted line), and in eastern Canada during August/September (broken line). The slope for Canada is statistically different from the others (see text).

uations to the 15-day period of maximum mass gain at each site. This analysis (Fig. 5) suggests that mass increase rates, illustrated by the *r*-values, were similar during northward migration at Lagoa do Peixe in Brazil and at Cheyenne Bottoms, United States, even though the birds in Brazil were, on average, substantially heavier than in Kansas. The slopes of these two lines were not statistically different from each other ($P > 0.05$). In contrast, the rate of mass increase during autumn was lower ($P < 0.001$) at the Magdalen Islands in Canada.

Our census and the available literature suggest that the overall timing of northward White-rumped Sandpiper migration is more rapid than the southward migration, even if comparisons are restricted to adult birds. For example, peak southward migration of adults in the Magdalen Islands is during August/September, about two and one-half months before major population buildup south of the Equator. On the other hand, major emigration from southern latitudes begins just a month and a half before spring settlement in breeding areas. The limited information presented

here (Fig. 5) also suggests that the fat deposition needed for rapid migration also occurs more rapidly during northward than during southward migration. For many, and perhaps most birds, this fattening occurs at widely separated, strategic sites which are potentially critical to the world populations of this remarkable migrant (cf. Myers et al. 1987).

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SEASONALITY, HABITAT USE, AND FLOCK SIZES OF SHOREBIRDS AT THE BAHÍA DE ASUNCIÓN, PARAGUAY

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ABSTRACT.—Twenty species of shorebirds were recorded during 47 censuses along the margins of the Paraguay River at the Bahía de Asunción, Paraguay, from 1987–1989. The numbers of most Nearctic migrants (15 species) were higher during boreal fall than during spring, presumably due to flooding of the Paraguay River basin during spring and summer; numbers of Neotropical residents (five species) peaked during December–March. The abundance of most shorebirds, especially Neotropical species, was correlated negatively with water level, an inverse measure of habitat availability. Interannual variation in abundance appeared to be related to local hydrological conditions. Each species differentially exploited a given habitat, providing evidence of habitat partitioning. Intraspecific flock sizes of most species were correlated with abundance and, by inference, seasonality and habitat availability. The evolution of Nearctic shorebird migration in the interior of South America appears to have been influenced by seasonal cycles of precipitation and the effects on habitat availability. *Received 19 Feb. 1991, accepted 20 June 1991.*

RESUMEN.—Se registraron 20 especies de playeros durante 47 censos a lo largo de los márgenes del río Paraguay en la bahía de Asunción, Paraguay, desde 1987 hasta 1989. La mayoría de migrantes neárticos (15 especies) alcanzaron números más altos durante el otoño boreal que durante la primavera, presumiblemente a causa de las inundaciones de la cuenca del río Paraguay durante la primavera y el verano; los residentes neotropicales (cinco especies) alcanzaron números más altos durante diciembre–marzo. La abundancia de la mayoría de playeros, especialmente los neotropicales, fue correlacionada negativamente con el nivel de agua, una medida inversa de disponibilidad de hábitat. La variación interanual en abundancia pareció estar relacionada con las condiciones hidrológicas locales. Cada especie explotó un cierto hábitat en una manera diferente, proveyendo evidencia de la partición de hábitat. Los tamaños de las bandadas intraespecíficas de la mayoría de las especies fueron correlacionados con abundancia y, por inferencia. estacionalidad y disponibilidad de hábitat. La evolución de migración por los playeros neárticos en el interior de Sudamérica parece haber afectado por ciclos estacionales de precipitación y los afectos sobre la disponibilidad de hábitat.

Although our knowledge of the distribution and abundance of Nearctic shorebird migrants along the coasts of South America is fairly extensive (Morrison and Ross 1989), studies of seasonality and habitat use of mixed assemblages of shorebirds in South America have been confined thus far

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to coastal areas in Peru (Hughes 1979, Duffy et al. 1981), Venezuela (McNeil 1970), Surinam (Spaans 1978), southern Brazil (Harrington et al. 1986, Vooren and Chiaradia 1990), Argentina (Myers and Myers 1979), and inland in central Venezuela (Thomas 1987) and eastern Peru (Bolster and Robinson 1990). There are no published quantitative studies of migrant shorebird populations from the interior of South America south of the Amazon basin.

On the basis of specimen records and anecdotal observations, Antas (1983) inferred that far fewer Nearctic shorebird migrants pass through the interior of South America during boreal spring migration than in autumn. This was thought to be related to differences in the quantity of precipitation during these periods and their effects on the hydrological basins. In most parts of central South America, rainfall is highest from November to March, thus flooding most river valleys when migrants are traveling northward toward their breeding grounds (Antas 1983). However, during the subsequent dry season, water levels fall rapidly along the major rivers and flooded lakes begin to dry up, thus creating a mosaic of mudflats, sandbars, and wet grasslands which collectively provide excellent habitat for southbound Nearctic shorebird migrants. The evolution of Nearctic shorebird migration in the interior of South America is thus postulated to have been influenced by seasonal cycles of precipitation and the resulting effects on habitat availability. However, there has been little quantitative evidence to support this hypothesis.

The status of Nearctic migrant shorebirds in the Republic of Paraguay, a land-locked country in south-central South America, was recently summarized by Hayes et al. (1990). Here we report the results of a two-year study on the seasonality and ecology of migrant and resident shorebirds at the Bahía de Asunción, Departamento Central, Paraguay. We focus on the differential seasonal use of the Bahía de Asunción by shorebirds and the effects of varying water levels on habitat availability, abundance, and flock sizes of shorebirds. We use our data to evaluate the hypothesis of Antas (1983) that Nearctic shorebird migration in the interior of South America has been influenced by seasonal cycles of precipitation and the effects on habitat availability.

STUDY AREA AND METHODS

Study area.—The Bahía de Asunción is a shallow bay of the Paraguay River situated along the northern outskirts of Asunción, the largest city in Paraguay (ca 800,000 residents). Roughly 4 km long and up to 2 km wide, the bay covers a variable surface area of 2–5 km^2. Because of the large amplitude of water level fluctuations along the Paraguay River, the width and depth of the bay vary greatly between seasons. However, day-to-day changes are small and usually unidirectional, with water level changes rarely exceeding 10 cm (Fig. 1;

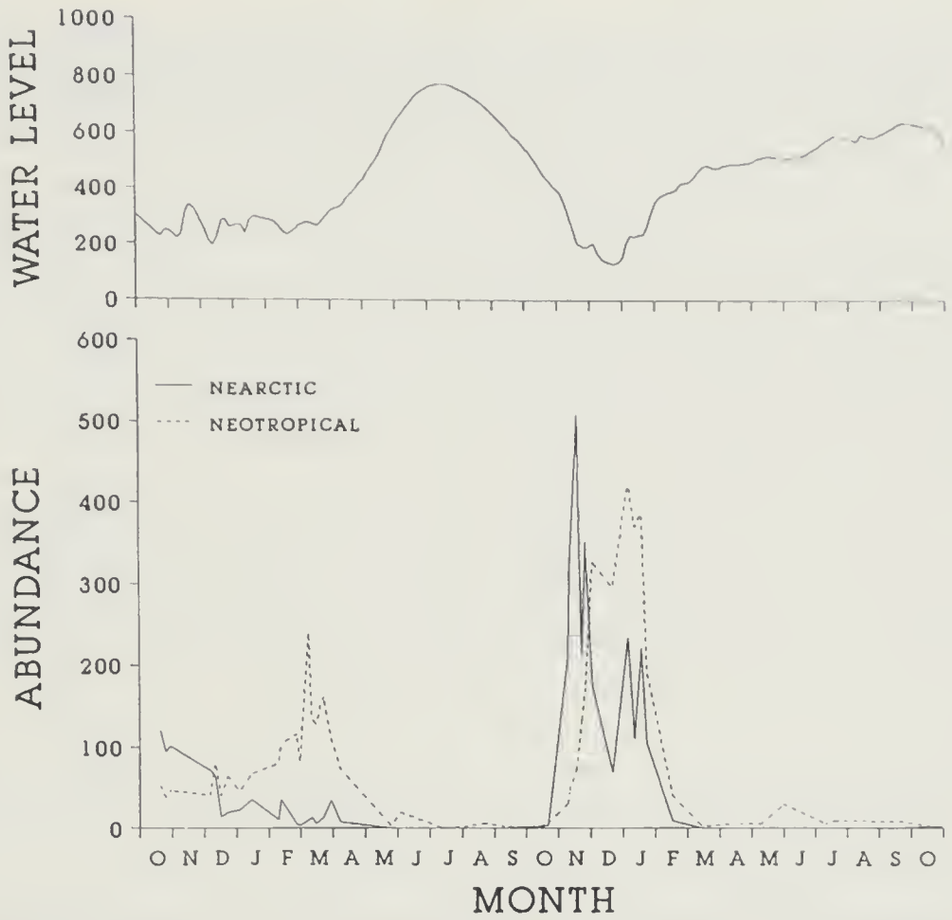

FIG. 1. Water levels (cm; zero point is arbitrary) and abundance of Nearctic and Neotropical shorebirds (all species combined for each group) at the Bahía de Asunción from October 1987 to October 1989.

unpubl. data). The southern and eastern banks of the bay are densely populated by humans, most of whom are poor squatters, and garbage is widely strewn in adjacent areas. The northern bank is lower in elevation and subject to inundation; it is inhabited by only a few families when water levels are low. Government buildings and a deep water port are located on both sides of the bay near its mouth at the western end. The bay is bordered on its northern and eastern edges by small patches of forest, several ponds, lagoons, marshes, and during periods of low water, extensive mudflats and fields.

Water levels at the Bahía de Asunción are usually highest during the dry season, from May to August, and lowest during the wet season, from November to January (Fig. 1). This results partly from the seasonal pattern of rainfall at the river's sources and partly from the inability of the river's drainage system to pass along immediately the large volumes of water it receives periodically in the form of precipitation (Anonymous 1985). Since 1978, flooding of the Paraguay River has reached unprecedented proportions, presumably due to the increased runoff of precipitation resulting from extensive deforestation in the river's watershed.

The widely fluctuating water levels of the Bahía de Asunción cause pronounced cyclical changes in the bay's physical appearance. During high water levels (>400 cm), much of the bay is under water with only the taller vegetation emerging above the surface. When the water recedes during the austral spring, the bay's emerging shoreline consists of bare mud. As the water continues to recede the upper shoreline dries out, and short grasses sprout, thus creating grassy fields except in several sandy or salty areas which remain barren. Sections of several lagoons transform into ponds as the water reaches its lowest levels; some ponds are choked with vegetation, whereas others continue to dry up and form large mudflats.

Grasses and sedges sprout along the water's edge when the water levels begin to rise again, eventually reaching a height of 0.5–1.0 m. When the water rises during the boreal spring, much of the shoreline transforms into a marsh, although several areas of bare soil still remain, especially at the upper levels of the bay. There is no published information on the limnology, botany, or invertebrate populations of the Bahía de Asunción.

Sampling methods.—From 20 October 1987 to 30 October 1989, we conducted 47 censuses of shorebirds at irregular intervals at the Bahía de Asunción. Up to five censuses were conducted each month except for November 1987 and June and August 1989; censuses were conducted more frequently during periods when shorebirds were common. During each census we covered the same areas of the bay on foot, rowboat, or by both methods. With the aid of 7× binoculars, we counted individual birds or estimated their numbers when in large flocks. All birds seen were counted, including those flying overhead; flying birds were identified either by their characteristic size and shape or, in the case of *Calidris* spp., by voice. Because of the highly variable amount of suitable shorebird habitat, we were unable to obtain densities based on the number of shorebirds per unit area. Most of the censuses (79%) were conducted during the morning. Censuses averaged 150 min in duration (range = 70–255 min); more time was required when large numbers of shorebirds were present.

In addition to counting birds, we recorded data on water levels, intraspecific flock sizes (number of individuals in a cohesive flock with a maximum distance of three m between individuals) and the habitat used by foraging individuals of each species. Data on water levels at the Bahía de Asunción were obtained from the Dirección de Hidrografía y Navegación of the Armada Nacional; water levels were used as an inverse measure of habitat availability (i.e., high habitat availability during low water, low habitat availability during high water). Three distinctive habitats occurred along a dry-wet gradient: dry land, wet land, and shallow water. The taxonomy of shorebird species mentioned in the text follows the A.O.U. check-list (1983) and Altman and Swift (1989).

Statistical analyses.—Spearman rank correlation coefficients (r_s-statistic; Siegel 1956) were used to compare shorebird abundance (number of individuals per count for a given species) with water levels and flock sizes. Mann-Whitney *U*-tests (*U*-statistic; Siegel 1956) were used to compare seasonal differences in the abundance of shorebirds during the periods of October–December and January–March (using only counts when mud or grass flats were exposed, with water level <400 cm), the abundance of shorebirds between the winters of 1987–1988 and 1988–1989 (using same criteria), and the correlations of abundance and water level between Nearctic and Neotropical species. All statistical tests were computed with *Statistix* software (Heisey and Nimis 1985). All probability values are two-tailed, with $\alpha = 0.05$.

RESULTS

Seasonality.—Twenty species of shorebirds were recorded during this study. Of these, 10 species were regularly occurring (>50 individuals recorded during study period) Nearctic migrants: Lesser Golden-Plover (*Pluvialis dominica*), Greater Yellowlegs (*Tringa melanoleuca*), Lesser Yellowlegs (*T. flavipes*), Solitary Sandpiper (*T. solitaria*), Upland Sandpiper (*Bartramia longicauda*), Hudsonian Godwit (*Limosa haemastica*), White-rumped Sandpiper (*Calidris fuscicollis*), Pectoral Sandpiper (*C. melanotos*), Stilt Sandpiper (*C. himantopus*), and Buff-breasted Sandpiper (*Tryngites subruficollis*). Five species of Nearctic migrants were rarely

observed (< four individuals during study period): Black-bellied Plover (*P. squatarola*), Spotted Sandpiper (*Actitis macularia*), Red Knot (*C. canutus*), Least Sandpiper (*C. minutilla*), and Sanderling (*C. alba*); accounts of these species were given by Hayes et al. (1990). Four species of resident Neotropical shorebirds were recorded regularly: Southern Lapwing (*Vanellus chilensis*), Collared Plover (*Charadrius collaris*), Black-necked Stilt (*Himantopus mexicanus*) and Wattled Jacana (*Jacana jacana*). Only five South American Snipe (*Gallinago paraguaiae*), a fifth species of Neotropical shorebird, were recorded. The data used in the statistical analyses were restricted to the 14 species of regularly occurring shorebirds at the Bahía de Asunción.

Seven species of regularly occurring Nearctic migrants appeared most commonly during the period of October to December, either occurring in small numbers or absent during January to April, even though suitable habitat was available: Lesser Golden-Plover, Greater Yellowlegs, White-rumped Sandpiper, Stilt Sandpiper, Upland Sandpiper, Hudsonian Godwit and Buff-breasted Sandpiper (Fig. 2); statistical tests supported this observation for all species but the Upland Sandpiper and Stilt Sandpiper (Table 1). Three species of Nearctic migrants occurred in fair numbers throughout the boreal winter: Solitary Sandpiper, Lesser Yellowlegs, and Pectoral Sandpiper (Fig. 2; Table 1). The numbers of all four species of regularly occurring Neotropical residents increased slowly during the months of October and November and peaked during December to March (Fig. 2). Statistical tests indicated that the Southern Lapwing and Collared Plover were more common during the period of January to March (Table 1). In contrast with the resident species, maximum counts of all Nearctic shorebird migrants combined were roughly twice as high prior to December than afterwards, even when water levels remained low (<400 cm) through early April 1988 (Fig. 1).

Interannual variation.—The abundance of all Nearctic shorebirds combined was much greater during the boreal winter of 1988–1989 (N = 12) than during 1987–1988 (N = 19; $U = 21.0$, $P < 0.001$; see Fig. 1). This pattern held true for six species of Nearctic shorebirds: Lesser Golden-Plover ($U = 21.0$, $P < 0.001$), Greater Yellowlegs ($U = 24.5$, $P < 0.001$), Lesser Yellowlegs ($U = 18.0$, $P < 0.001$), Hudsonian Godwit ($U = 47.5$, $P < 0.01$), Pectoral Sandpiper ($U = 13.5$, $P < 0.001$), and Stilt Sandpiper (absent during 1987–1988, data insufficient for analysis; see Fig. 2). However, the abundance of four species of Nearctic shorebirds did not vary between 1987–1988 and 1988–1989: Solitary Sandpiper ($U = 109.5$, $P > 0.85$), Upland Sandpiper ($U = 93.0$, $P > 0.40$), White-rumped Sandpiper ($U = 79.5$, $P > 0.15$), and Buff-breasted Sandpiper ($U = 85.0$, $P > 0.20$). Of the Neotropical shorebird species, only the Black-necked Stilt was

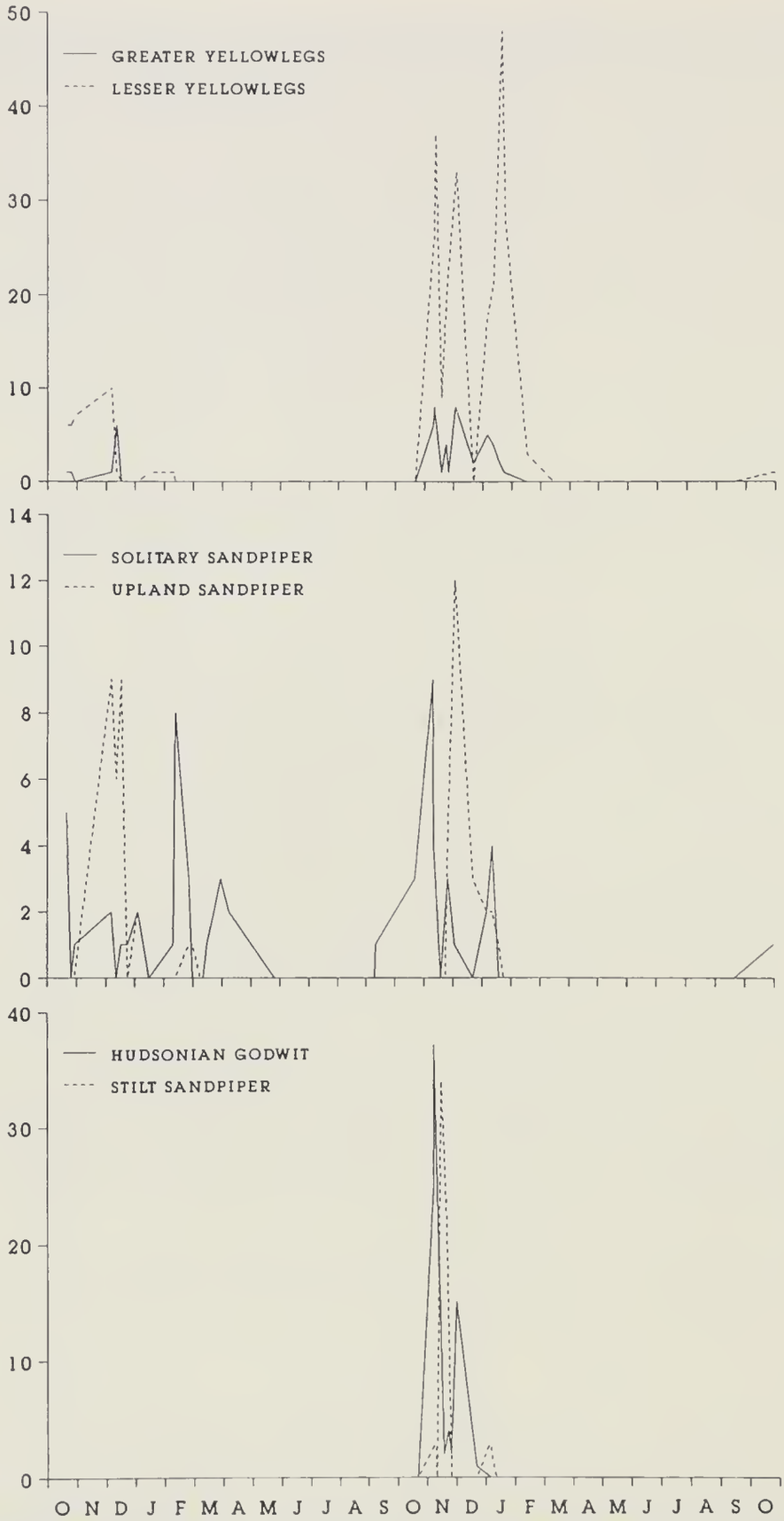

FIG. 2. Abundance (*y*-axis) of 14 species of shorebirds at the Bahía de Asunción from October 1987 to October 1989 (*x*-axis).

more abundant during the winter of 1988–1989 ($U = 6.0$, $P < 0.001$). The abundance of the other three species did not vary between 1987–1988 and 1988–1989: Southern Lapwing ($U = 111.0$, $P > 0.90$), Collared Plover ($U = 104.5$, $P > 0.70$), and Wattled Jacana ($U = 73.0$, $P > 0.10$;

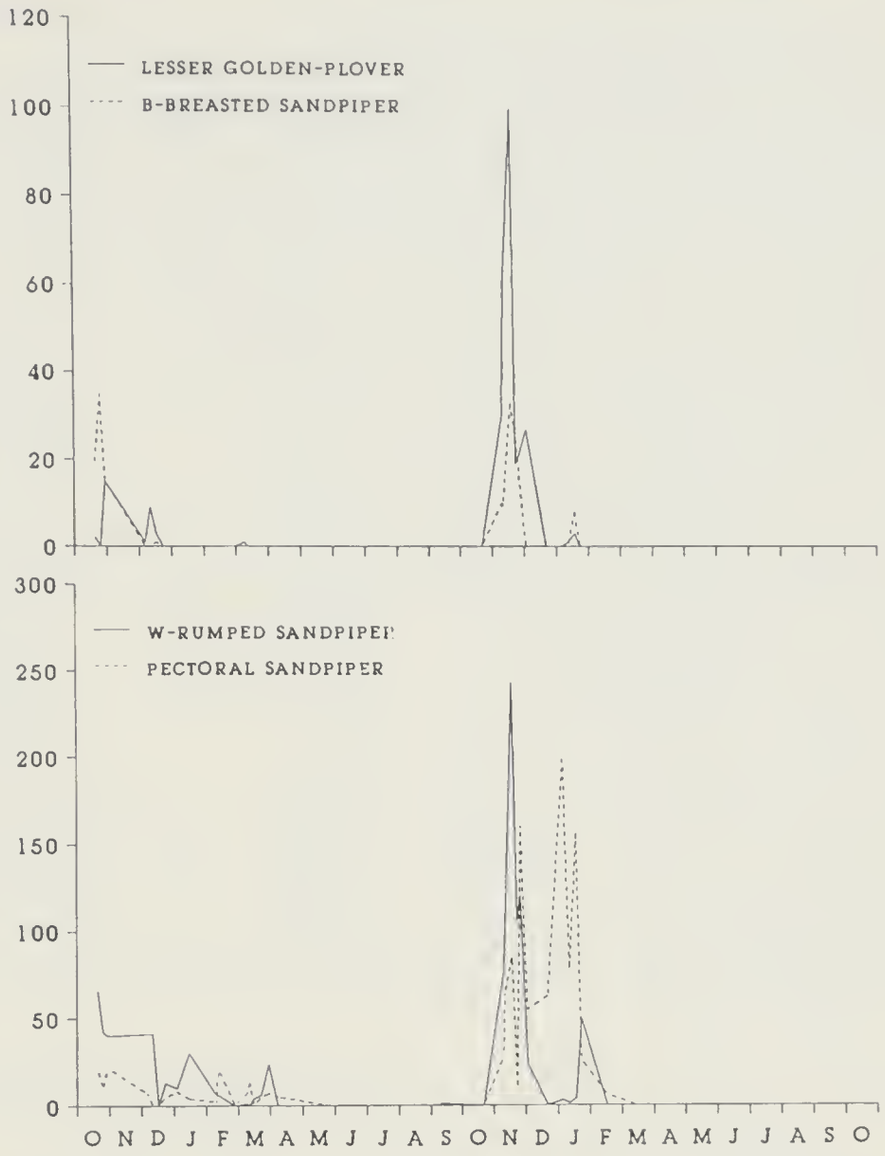

FIG. 2. Continued.

see Fig. 2). The abundance of all Neotropical shorebirds combined was greater during the winter of 1988–1989, but not quite significantly so ($U = 67.0$, $P = 0.059$; see Fig. 1).

Habitat use.—The abundance of all species of Neotropical shorebirds and five of the Nearctic migrant species was negatively correlated with water level (Table 1); i.e., the abundance of most species of shorebirds was directly proportional to the availability of habitat (exposed mudflats or fields). The correlation coefficients of resident species averaged higher than those of migrant species ($U = 2$, $P < 0.01$).

Although the 14 species of shorebirds overlapped greatly in their use of habitat, each species differentially exploited a given habitat along a dry-wet gradient (Fig. 3). The Wattled Jacana and Solitary Sandpiper appeared to overlap completely in habitat use (Fig. 3); however, the Wattled Jacana was the only species observed to forage on floating vegetation

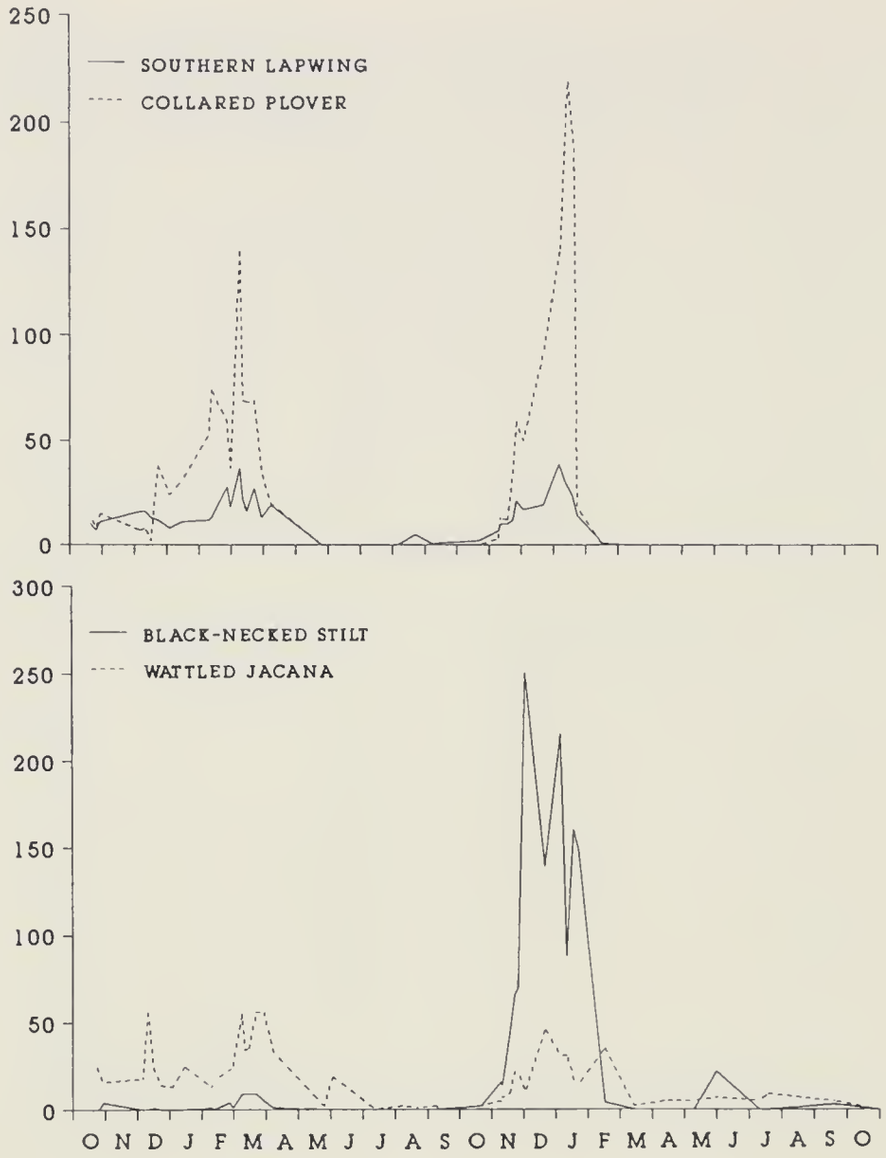

FIG. 2. Continued.

(used exclusively [100%] during periods of inundation but rarely [0.5%] when exposed land was available), a habitat not shown in Fig. 3.

Flock sizes.—Mean intraspecific flock sizes varied greatly between species, ranging from 1.3 birds/flock in the Solitary Sandpiper to 13.7 in the Black-necked Stilt (Table 2). Intraspecific flock sizes were correlated with abundance for all four Neotropical species, but only for half of the Nearctic migrant species (Table 2).

DISCUSSION

Seasonality.—This study demonstrates that many species of Nearctic shorebirds are absent or less abundant at the Bahía de Asunción during the boreal spring. Maximum counts of all Nearctic shorebird migrants combined were roughly twice as high prior to December than afterwards, even when water levels remained low through early April. Data from

TABLE 1

MEAN COUNTS OF SHOREBIRDS DURING PERIODS OF LOW WATER (<400 CM) DURING OCTOBER–DECEMBER (N = 14) AND JANUARY–MARCH (N = 16) WITH MANN-WHITNEY *U*-TEST COMPARING MEANS, AND SPEARMAN RANK CORRELATION COEFFICIENTS COMPARING SHOREBIRD ABUNDANCE WITH WATER LEVELS

Species	Oct.–Dec.	Jan.–Mar.	*U*	Water level r_s
Southern Lapwing	12.9	19.6	63.5*	−0.757***
Lesser Golden-Plover	20.5	0.3	32.0***	−0.267
Collared Plover	25.4	76.6	44.5**	−0.683***
Black-necked Stilt	43.1	41.4	106.5	−0.476**
Wattled Jacana	21.6	30.1	68.5	−0.648***
Greater Yellowlegs	2.8	0.8	51.5*	−0.374*
Lesser Yellowlegs	12.8	7.5	69.5	−0.376*
Solitary Sandpiper	2.1	1.6	98.5	−0.263
Upland Sandpiper	3.1	0.6	88.0	−0.319*
Hudsonian Godwit	6.1	0.0	56.0*	−0.093
White-rumped Sandpiper	64.6	9.1	37.5**	−0.509***
Pectoral Sandpiper	37.9	33.5	85.0	−0.638***
Stilt Sandpiper[a]	4.2	0.2	—	—
Buff-breasted Sandpiper	11.6	0.6	46.5**	−0.086

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
[a] Insufficient data (observed during only four censuses).

specimen records and observations from other areas in Paraguay indicate that most Nearctic shorebird species are less abundant during northbound migration even in areas away from the Paraguay River (Hayes et al. 1990; Hayes, unpubl. data).

The northbound route(s) used by these Nearctic migrants is unknown; most likely they either migrate northward along the Atlantic coast or fly nonstop through central South America until they reach the Carribean or Atlantic coasts or nearby inland areas (Antas 1983). Large concentrations of spring migrants have been reported along the Atlantic coast of southern Brazil (Harrington et al. 1986, Vooren and Chiaradia 1990) and in the interior of Venezuela (Thomas 1987). In contrast with Paraguay, the availability of habitat in the interior of Venezuela is apparently greater during boreal spring than during fall (Thomas 1987). The data from the Bahía de Asunción and elsewhere support the hypothesis of Antas (1983) that the evolution of migration by Nearctic shorebirds in the interior of South America has been influenced by seasonal cycles of precipitation and the resulting effects on habitat availability.

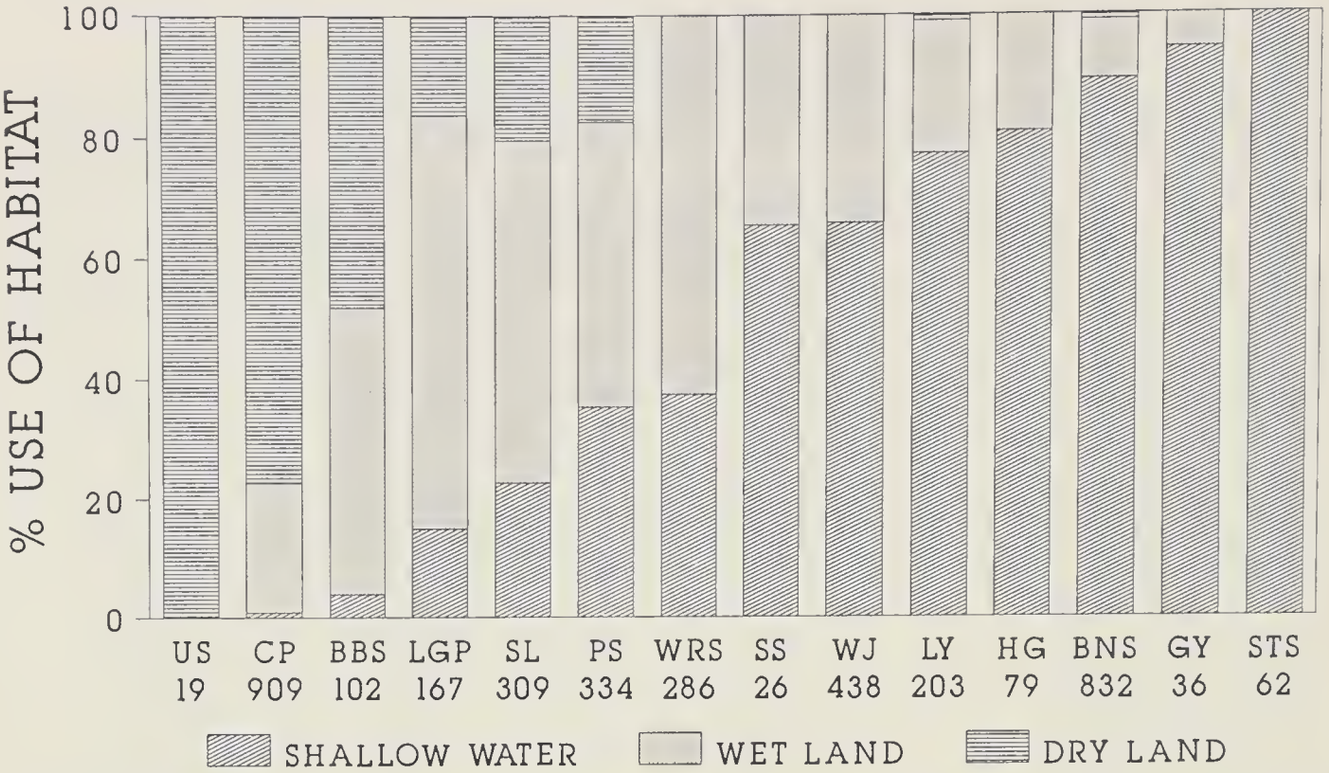

FIG. 3. Percent habitat use of shorebirds at the Bahía de Asunción, with N values below. US = Upland Sandpiper; CP = Collared Plover; BBS = Buff-breasted Sandpiper; LGP = Lesser Golden-Plover; SL = Southern Lapwing; PS = Pectoral Sandpiper; WRS = White-rumped Sandpiper; SS = Solitary Sandpiper; WJ = Wattled Jacana; LY = Lesser Yelowlegs; HG = Hudsonian Godwit; BNS = Black-necked Stilt; GY = Greater Yellowlegs; STS = Stilt Sandpiper.

The numbers of shorebirds occurring at the Bahía de Asunción and other areas in the interior of South America (e.g., Dott 1985, Thomas 1987, Bolster and Robinson 1990, Hayes et al. 1990) are small in comparison with the numbers reported along coastal areas (Morrison and Ross 1989). Although large numbers of migrant shorebirds apparently pass through the interior of South America, they are widely dispersed; there are no known "staging areas" (Myers 1983) in need of special protection.

Interannual variation.—The larger concentrations of shorebirds observed during the boreal winter of 1988–1989 do not appear to be related to the availability of habitat at the Bahía de Asunción, and no information is available on the abundance or availability of food resources. We suspect that the larger concentrations in 1988–1989 may have resulted from a lack of available habitat elsewhere in the Paraguay River watershed. Because of a long, extended drought during the autumn of 1988, many wetland areas away from the Paraguay River (e.g., in the Chaco) dried up (pers. obs.). If these wetlands host shorebird populations during normal years, then during a drought shorebirds might be expected to concentrate

TABLE 2

FLOCK SIZES OF REGULARLY OCCURRING SHOREBIRDS AT THE BAHIA DE ASUNCION WITH SPEARMAN RANK CORRELATION COEFFICIENTS COMPARING FLOCK SIZE WITH ABUNDANCE

Species	Flock Size				Abundance
	N	$\bar{x}$	SD	Range	r_s
Southern Lapwing	206	2.2	1.9	1–15	0.189*
Lesser Golden-Plover	49	5.2	7.9	1–50	0.155
Collared Plover	224	5.6	11.4	1–94	0.212*
Black-necked Stilt	82	13.7	24.5	1–174	0.301*
Wattled Jacana	185	3.7	4.3	1–32	0.216*
Greater Yellowlegs	29	1.7	1.4	1–7	0.560*
Lesser Yellowlegs	63	4.1	4.9	1–21	0.196
Solitary Sandpiper	43	1.3	1.0	1–5	0.566**
Upland Sandpiper	18	2.4	2.3	1–9	0.801**
Hudsonian Godwit	14	5.6	6.0	1–18	0.378
White-rumped Sandpiper	68	12.1	20.4	1–125	0.419**
Pectoral Sandpiper	144	5.8	11.7	1–120	0.255*
Stilt Sandpiper	9	6.9	6.6	2–22	0.271
Buff-breasted Sandpiper	36	4.8	3.9	1–17	0.229

* $P < 0.01$.
** $P < 0.001$.

in suitable habitat along the Paraguay River and larger bodies of water away from the river. Quantitative evidence supporting this hypothesis comes from a shorebird census conducted by Hayes (unpubl. data) at two small ponds and a flooded field (roughly 0.02 km^2) at Guarambaré, Departamento Central, an agricultural community situated about 9 km east of the Paraguay River and 28 km southeast of the Bahía de Asunción.

Habitat use.—The abundance of shorebirds at the Bahía de Asunción during a given year is clearly related to the availability of habitat, especially for Neotropical residents, as indicated by the correlations with water level. The lower correlation coefficients of Nearctic migrant species are indicative of their more transient appearance in Paraguay. Many species of migrants apparently winter farther south (Myers and Myers 1979, Morrison and Ross 1989) despite an abundance of suitable habitat at the Bahía de Asunción throughout the boreal winter. Although some species overlapped greatly in their habitat use, the differential use of habitats by each shorebird species along a dry-wet gradient provides evidence of habitat partitioning while at the Bahía de Asunción.

Flock sizes.—Burger and Gochfeld (1983) found that flock sizes of shorebirds were influenced by location, activity (roosting, foraging), date,

and environmental variables such as tide, cloud cover, temperature, and wind. The presence or absence of a predator also affects the sizes of shorebird flocks (Myers 1984). Our findings indicate that flock sizes of certain species are influenced by abundance and, by inference, seasonality and availability of habitat.

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SPECIMENS AND PROBABLE BREEDING ACTIVITY OF THE BAND-RUMPED STORM-PETREL ON HAWAII

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ABSTRACT.—Specimens (a downy fledgling and a hatch-year juvenile) and nocturnal calling of the Band-rumped Storm-Petrel (*Oceanodroma castro*) are evidence that this rare seabird breeds on the island of Hawaii. Nocturnal calling over land and sightings near the coast indicate that populations nest on the southwest rift and possibly the upper western slope of Mauna Loa. *Received 12 Feb. 1991, accepted 1 July 1991.*

The Band-rumped Storm-Petrel (*Oceanodroma castro*) breeds on widely separated islands in and around the margins of the tropical Atlantic and Pacific oceans (Palmer 1962). Nests of *O. castro* in the Pacific have been found on Hide Shima and Sangan Jima off the east coast of Japan and on several of the Galapagos islands (Cramp and Simmons 1977, Harris 1982, American Ornithologists' Union 1983, Harrison 1983). *Oceanodroma castro* is the rarest seabird thought to breed in the Hawaiian Islands, where its breeding distribution is poorly known (Harrison et al. 1990). It probably breeds on the island of Kauai, where fledglings have been collected, and possibly on Maui, but nests or eggs have not yet been found in the Hawaiian Islands (Richardson 1957, Munro 1960, Berger 1981, American Ornithologists' Union 1983, Pratt et al. 1987, Harrison 1990, Harrison et al. 1990).

Oceanodroma castro probably occurred on all main Hawaiian islands prior to Western contact (A. C. Ziegler, pers. comm.); its fossil remains were found on Oahu and Molokai by Olson and James (1982). Remains recovered from many Polynesian middens on the island of Hawaii indicate that the species was once common enough there to constitute a noticeable part of the early Hawaiians' diet (A. C. Ziegler, pers. comm.). There are no accounts of specimens or breeding on the island of Hawaii following Western contact in 1778 (Wilson and Evans 1890–1899, Perkins 1903, Rothschild 1893–1900), although Henshaw (1902) noted that native Hawaiians reported *O. castro,* known to them as 'Ake'ake, to be "common on the fishing grounds five or ten miles off the windward [northeast] coast

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of Hawaii." Berger (1981) noted that "immature birds were found on Hawaii and Kauai in the past," but he provided no further evidence of specimens or breeding on Hawaii. We report herein on the first specimens of this species from Hawaii Island and circumstantial evidence that the bird nests there.

SPECIMENS

In April 1967, W. E. Banko identified a small storm-petrel with natal down in the Hawaii Volcanoes National Park bird specimen collection as the first specimen of *O. castro* from the island of Hawaii. John W. Aldrich (pers. comm.) confirmed the identification and deposited the specimen in the National Museum of Natural History (USNM specimen #529770). The specimen label reads, "October 28, 1949. D. H. Hubbard 510, Motor Pool, Kilauea Military Camp, H.N.P." The bird was found near a woven wire fence at the Kilauea Military Camp motor pool near the rim of Kilauea Crater at 1219 m elevation (Fig. 1). It may have collided with the fence after having been attracted or confused by lights at the camp. *O. castro* is known to be attracted to lights at night (Harrison 1990). Another seabird, the Hawaiian (Dark-rumped) Petrel (*Pterodroma phaeopygia*), occasionally has crashed in the vicinity of lights around the summit area of Kilauea Crater (pers. obs.).

Because storms or unusual winds were not detected in the main Hawaiian Islands during October 1949 (Anonymous 1949), the specimen of *O. castro* probably was not blown to Hawaii from another island. Local weather at the time (National Park Service weather records) consisted of normal NE trade winds, partly cloudy skies, and light precipitation.

W. E. and P. C. Banko discovered most of a bird on the southwest rift of Mauna Loa near a line of volcanic vents about 1.6 km north of Puu O Keokeo (USGS quadrangle map: PUU O KEOKEO) at 2103 m elevation (Fig. 1) on 11 July 1968. The wing was that of *O. castro* (R. C. Laybourne, R. C. Banks, pers. comms.), but it was not saved as a voucher specimen. We also found two feathers from *O. castro* during 25–28 August 1973 in front of an apparent nest burrow entrance about 1.6 km from the wing specimen. These feathers were lost after they were sent to the U.S. National Museum, and their identity could not be confirmed.

On 3 November 1988, R. E. David examined and identified a live individual of *O. castro* that was discovered at Kulani Correctional Facility (1585 m elevation on the eastern slope of Mauna Loa about 14 km N of Kilauea Military Camp; see Fig. 1). This bird probably was confused by lights at the prison and crashed into the side of a building during the week of 20 October 1988. Unusual weather was not reported during this period (Anonymous 1988; National Weather Service, Honolulu Weather Service

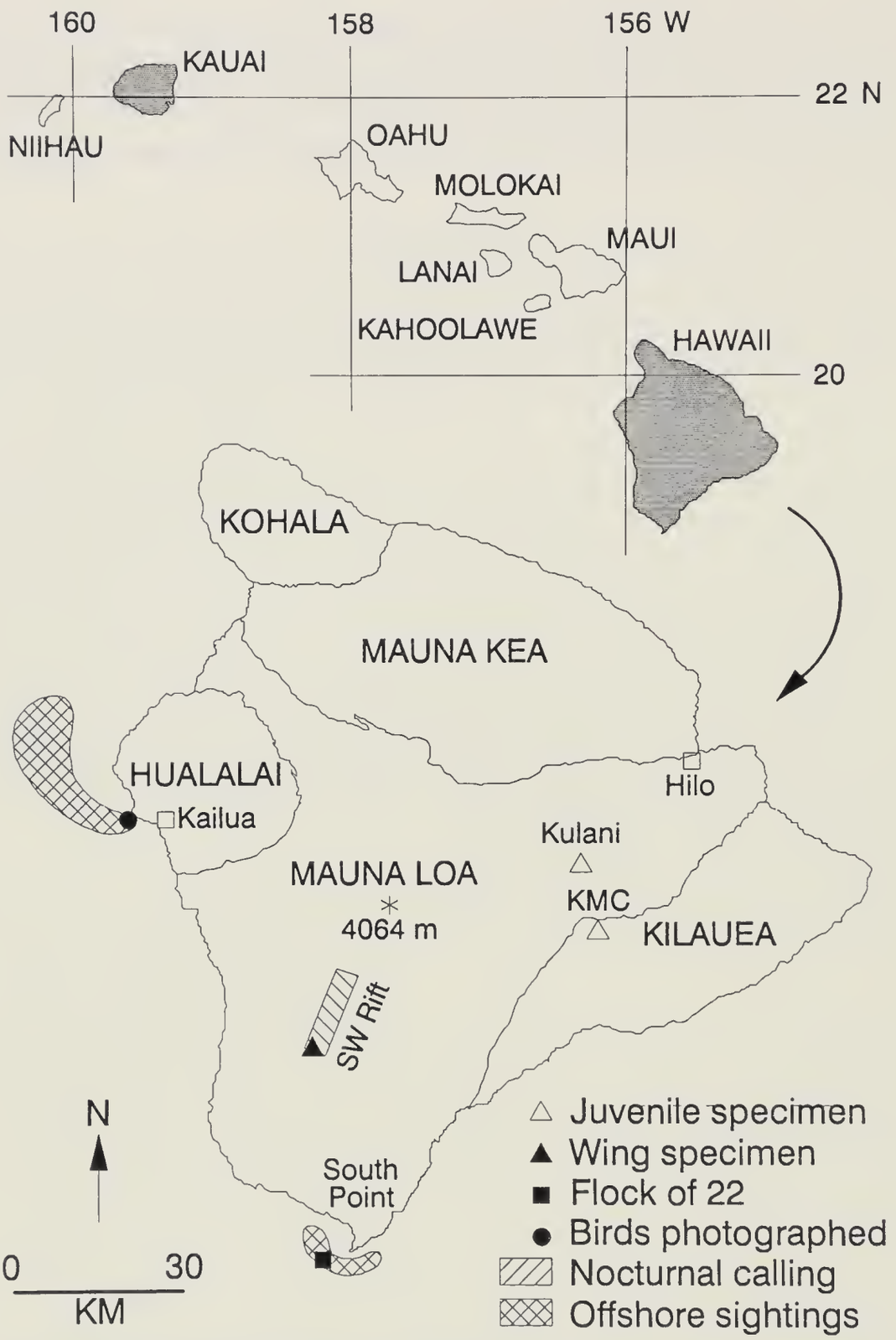

FIG. 1. Location of *Oceanodroma castro* records in the Hawaiian Islands. Breeding is believed to occur on Kauai and Hawaii (shaded).

Forecast Office, unpubl. data). State wildlife officials delivered the bird to the Panaewa Zoo in Hilo on 24 October and transferred it to Hilo Veterinary Clinic on 31 October, at which time it weighed 30 g (M. Lepes, pers. comm.). This weight is considerably below average for the species (42–44 g for adults and 49 g for fledglings; Cramp and Simmons 1977), indicating that the bird lost weight prior to its delivery to the veterinary

TABLE 1
TIMES AND ELEVATIONS OF *OCEANODROMA CASTRO* CALLS HEARD ON SOUTHWEST RIFT OF MAUNA LOA

Date	Time	Elevation (m)
25 June 68	20:05–22:30	2134
26 June 68	20:30–20:40	2377
10 July 68	20:35–22:30	2231
25 July 68	20:15	2530
25 August 73	>20:00	2957
26 August 73	>20:00	2469
27 August 73	>20:00	2246
28 August 73	>20:00	2096

clinic. It weighed only 21 g when it died in captivity on 18 November 1988; necropsy revealed no cause of death other than malnutrition (M. Lepes, pers. comm.).

The gonads of this specimen were inconspicuous, and the bird's sex could not be determined (M. Lepes, pers. comm.). Although the specimen lacked natal down, we believe it was a juvenile because the scapulars were edged with white (Palmer 1962, Cramp and Simmons 1977), the gonads were not well-developed, and it was recovered in October, when other Hawaiian fledglings of this species have been found (Richardson 1957, this paper). The specimen was preserved as a skin and partial skeleton at the Bernice Pauahi Bishop Museum (BPBM specimen #177920). Body measurements (R. L. Pyle, pers. comm.) were culmen 13.2 mm, tarsus 22.6 mm, and wing chord 140 mm (145 mm flattened).

OBSERVATIONS

W. E. and P. C. Banko heard calls of *O. castro* at 2096–2957 m elevation at volcanic cones along the southwest rift of Mauna Loa in 1968 and 1973 while conducting nocturnal surveys for the U.S. Fish and Wildlife Service (Table 1). These rapid, high-pitched, chattering calls, recorded as "kee-kee-kee" and resembling the sound of rubbing a wet finger over glass (Pratt et al. 1987), were easily distinguished from those of *P. phaeopygia*, which we also heard at night on the southwest rift below 2245 m elevation (Banko 1980).

Recently, R. E. David has regularly seen solitary Band-rumped Storm-Petrels from May through July within about 5 km of the west and southwest coast of Hawaii between Kailua and South Point (Fig. 1). He photographed two individuals flying southward, and these photographs are

maintained jointly by the Hawaii Audubon Society and Bishop Museum in the Hawaii Rare Bird Photographic File (HRBP #766–768 and #860–862). He photographed one bird on 7 May 1985 about 4.8 km west-northwest of Kailua, and the other was observed on 26 July 1986 about 4 km west of Kailua.

David has also seen flocks of *O. castro* at sea during September and October, including a flock of 22 birds 5.6 km west of South Point on 10 October 1988. Local fishermen report seeing this species regularly off South Point during the early fall.

DISCUSSION

The seemingly common and widespread population of *O. castro* inhabiting the island of Hawaii during the Polynesian era probably became restricted to very high elevation breeding grounds during the past two centuries of Western colonization. Our observations suggest that a breeding population persists on the upper slopes of Mauna Loa. Evidence includes specimens of two juvenile birds, nocturnal calling over inland habitat during the breeding season, and sightings of individuals and flocks close to shore. Because this species ranges close to its breeding grounds (Naveen 1982, American Ornithologists' Union 1983), recent sightings just off the west coast and southern tip of Hawaii suggest that the species continues to nest on the southwest rift and western slopes of Mauna Loa.

We recommend that the breeding areas and populations of this species be precisely determined, studied, and protected. We also suggest that surveys for breeding birds be concentrated high on Mauna Loa around volcanic cinder cones, where the substrate affords easy burrowing, and in lava tubes and highly fractured lava flows, where cavities exist for nesting.

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SHORT COMMUNICATIONS

Copulatory and other pre-incubation behaviors of Cooper's Hawks.—Data on pre-incubation behavior of falconiforms are scarce, and Brown and Amadon (1968) and Palmer (1988) give the only descriptions of pre-laying activities of the Cooper's Hawk (*Accipiter cooperii*). Their descriptions are based on Meng (1951), who provides an unquantified narrative summary of activities during this stage. Here we present a quantitative analysis of copulatory and related pre-incubation behaviors obtained over four breeding seasons.

Methods.—We observed pre-incubation behavior in 47 mated pairs of Cooper's Hawks at 28 nesting areas in Wisconsin during 24 March–19 April 1986 (9 pairs), 7–24 April 1987 (12 pairs), 26 March–5 May 1988 (16 pairs), and 23 March–12 May 1989 (10 pairs). Identification of nesting areas was based on an 11-year data set (Rosenfield and Bielefeldt, unpubl. data). Based on capture and re-capture data for marked birds, we believe a minimum of 46 different adults (28 males, 18 females) were involved. All observations were made after pair formation, and all mated pairs laid eggs. We watched Cooper's Hawks at partially constructed nests during 84 observation periods (20 in 1986, 18 in 1987, 27 in 1988, and 19 in 1989). Observations totaled 7325 min ($\bar{x}$ = 87 min/episode, range = 16–326 min) mostly (N = 69 or 82%) beginning with the day's first arrival (04:30–05:15 h CST) of an adult near a nest. These are termed "early morning periods" (hereafter "early"), most (63 or 91%) of which ended at or before 08:30. Observations (N = 15) at other times of the day (hereafter "later") began after 08:30 (08:31–18:20). Early morning and later observations made up 73% (5327 min) and 27% (1998 min) of the total observation time, respectively. Our previous fieldwork (1980–1985) indicated that the hawks were predictably present on nesting areas at dawn. More time was spent on early morning observations when we expected greater frequency (and higher variance) for the behaviors considered here.

All components of behavior were not equally observable, and thus sample sizes vary. Unless the terms "separate" or "different" are explicitly applied to individuals, pairs, or nests, samples include multiple observations of the same individual birds. Birds in the same nesting area in different years are treated as separate cases. The hawks were sexed by size (males are markedly smaller) and vocalizations (females called more frequently and had larger repertoires [Rosenfield and Bielefeldt 1991]). We standardized the analyses of copulations, nest visits, and twig deliveries to partially constructed nests as number per hour.

Because it was impossible to determine whether sperm was transferred during copulation, we defined a copulation as occurring when a male mounted a female. Statistical analyses follow Cochran (1977) and Zar (1984). Significance was accepted at the 0.05 level. For a more detailed description of study area and methods see Rosenfield (1990).

Results and discussion.—Cooper's Hawks were not seen on nesting areas until mid-March, and eggs were laid in late April–early May. The pre-incubation period was thus at least 30 days. During the pre-incubation period, male Cooper's Hawks, like other raptor species (Newton 1979), leave the nesting area to hunt during some part of the day, while females remain near the nest. We never saw (1) either sex hunt near the nest, (2) females depart the nesting area and leave males unattended, or (3) females arrive at a nesting area with food. When we saw males depart the nesting area (N = 15) and leave females unattended, or at other times when unattended females were found on nesting areas (N = 4), returning males (N = 9 different birds) always arrived with prey. Females were present for 99% of 6200 min in which we could account for the presence of at least one bird on the nesting area, males for 80%. Males were more likely to be absent from nesting areas in later periods than in early morning periods. Pooled data for total observational time show males were absent for

458 of 1531 min (30%) in later periods and 782 of 4669 min (17%) in early periods, but both of these proportions are skewed by extended absences of a few individual males. Treating observation periods as independent, we found that mean proportion of time absent in 13 later periods was 21%, but only 9% in 64 early periods. Males are more likely to be present on nesting areas during the early morning hours and for a large proportion of the time at all hours of the day.

We observed 120 copulations: 23 among eight pairs of Cooper's Hawks in 1986, 24 among nine pairs in 1987, 42 among fourteen pairs in 1988, and 31 among six pairs in 1989. Copulations occurred throughout the pre-laying period with no apparent peaks in copulatory activity during this time (see Rosenfield 1990). During at least 45 (38%) copulations, both birds gave multi-noted "whaaa" calls (see spectrograph in Rosenfield and Bielefeldt 1991), and on at least 15 other occasions (12%), only the female called. At least one bird always called during all copulations. Fifty-seven copulations in our study averaged 4.5 sec in duration (range = 2–6 sec). All copulations, except one that occurred on the ground while a female was feeding, occurred in trees at distances of 20–80 m from the nest and at heights of 2–15 m. Males always (N = 102) flew toward females to copulate, never the reverse.

The incidence of copulations is strongly associated with nest buildings by males. Among 102 copulations in which we clearly saw the male before mounting, he had visited the nest ≤1 min earlier on 82 occasions (80%). On 71 (70%) occasions, the male flew directly from the nest to the female without perching in the interim. On two of these 71 occasions, two different males gathered twigs and then attempted to copulate en route to the nest, but females seemed to reject copulation until after the males had visited the nests. In two other instances, two separate males that had unsuccessfully tried to break twigs flew immediately to their mates and copulated. Of the five times in which we saw females (N = 4 different birds) solicit copulations by tilting to a horizontal position when males were about 3–5 m away, all occurred while males were departing nests.

Copulations were also associated with courtship feeding. Copulations followed all but one of 10 cases in which different males provided prey to females. Eight different males each copulated once, and another male twice, while their mates were feeding. These copulations also immediately followed nest visits by males.

The total number of copulations per clutch is not known, but an estimate can be derived from the copulation rate. Copulations occurred throughout the day, but early morning rates were significantly higher than later rates (Mann-Whitney $U = 556.5$, $P = 0.003$). The copulation rates observed in our study were weighted according to available daylight hours in the pre-incubation period in stratified sampling of early and later strata (see Table 1), and the resulting estimate of number of copulations in the 30-day period prior to egg laying was 372 ± 184 (95% confidence interval).

In early morning observation periods (N = 69), the hawks vocalized at the nest site at dawn, 5–25 min before sunrise. On all but two occasions, both sexes called upon their arrival at dawn. We do not know where the hawks had roosted, but when visible to us (N = 15), 12 different males arrived from elsewhere before calling. Males' initial calling posts were 25–150 m from the nests (N = 17 separate individuals). Females' initial calling positions were difficult to determine because many called in flight while approaching the nesting area. We estimate, however, that the range of female-to-male distances at initial dawn calls was similar to that for male-to-nest distances. Median male-to-female distances at initial calls was 60 m (N = 28).

Females flew toward nests (N = 15) or male calling posts (N = 20) within 5–120 sec (median = 15 sec) of the initial calls by either bird, and male approach to female (N = 1) or mutual approach (N = 1) was rarer. Both sexes called frequently before and during these approaches, and this "exchange" of calls continued for 5–1050 sec (median = 120 sec).

Table 1

Estimated Number of Copulations per Clutch[a] for Cooper's Hawks in Wisconsin, Based on Stratified Sampling

Stratum	Total possible pair-year-h[b]	Total h[c]	Stratum mass	Mean copulations/h	Sample variance
Early obs.	22,560	65	29%	1.69	2.77
Later obs.	56,400	13	71%	0.56	0.99
Totals	78,960	78			
Stratified mean/h			0.89		
Stratified variance (of the mean)			4.19		
SE			0.20		

At the 95% confidence interval (14 df), estimated number copulations per clutch = 372 ± 184

[a] Based on estimated 30 days of copulation prior to incubation.
[b] Based on 14-h day × 30 days per pair × 47 pairs × four seasons.
[c] Standardized copulations/h based on variable-length observation periods, see text.

From 1.0–34.0 min (median = 8.4) after initial calls at dawn, visits to the nests began. We avoid the term "nest building" for the first nest visit of the day because birds carried no building material in at least nine instances. Males made 82% (N = 56) ($\chi^2 = 23.2$, df = 1, $P < 0.001$) of the initial morning nest visits.

At least one bird made a minimum of one visit to a partially constructed nest in 78 of 84 (93%) observation periods. On seven of these 78 observation periods, we could not determine the sex of a bird on a nest visit. We separated number of nest visits from number of twig deliveries because frequently we could not see whether a bird carried a twig on each visit. Both sexes built, and males made 69% of visits to partially constructed nests in early and later periods combined. This value is the mean of proportions of male nest visits at each nesting area in each year (N = 43), with a total of 542 nest visits by both sexes. Sign tests show that males made significantly more nest visits ($P < 0.001$, N = 41) *and* significantly more twig deliveries ($P < 0.01$, N = 30) than females in combined early and later periods (see Rosenfield [1990] for a breakdown of nest visits and twig deliveries by males and females for each nesting area).

In addition to absolute number of nest visits and twig deliveries, we evaluated rates of visits and deliveries (per h). Males exhibited a significantly higher nest visit rate (Mann-Whitney $U = 3474$, $P < 0.001$) and twig delivery rate ($U = 3159$, $P = 0.019$) than females for all observation periods combined.

Visits by male and female Cooper's Hawks to partially constructed nests occurred throughout the pre-laying period (see Rosenfield 1990). As with copulations, there was marked diurnal variation in nest building. Except for a marginally non-significant difference (Mann-Whitney $U = 484.5$, $P = 0.054$) in the diurnal variation in twig delivery rate for males, intrasexual nest visit rates to uncompleted nests were significantly higher during early observation periods than during later periods (Mann-Whitney $U = 568.0$, $P = 0.002$, and $U = 593.5$, $P = 0.01$, for male and female nest visit rates, respectively; and $U = 555.5$, $P = 0.002$ for twig delivery rate by females).

Our data indicate that males do at least twice as much building as do females. On some nest visits, as Meng (1951) suggests, females (or males) may only be "inspecting" the nest or "rearranging" twigs. We could not determine the frequency or sexual apportionment of non-building visits to the nest in all observation periods. However, in 39 periods where we saw birds clearly, males and females delivered twigs on 279 of 296 (94%) and 105 of 126

(83%) nest visits, respectively, while males (seven different birds) and females (minimum of five different birds) made at least seven and 16 visits without twigs, respectively. Thus a maximum of 6% of nest visits by males and 17% of visits by females could have been without twigs. We believe that these frequencies are representative of all observation periods.

Although nest building essentially occurred only when both members of a mated pair were present, only one bird built at a time while the other bird perched nearby. We never saw both birds gathering twigs at the same time. Of 542 visits to partially constructed nests, 534 (99%) occurred when both male and female were present. During one early observation period, an unattended male (the only instance in which a male was observed alone) made seven visits to a nest (all with twigs) during 25 min before we detected his mate. We saw only one nest visit (without a twig) among at least 12 different females during 20 h at 15 nests.

We watched Cooper's Hawks gather 331 twigs (235 by males and 96 by females), representing 77% of the 429 observed twig deliveries. All twigs (except two, one taken by a male from the ground, and one from a tree while in flight) were collected in trees by perched hawks using their beaks. Excluding alternate nest building (see below), all observed twig collections occurred within 20–80 m of the nest, most (N = 214 [65%]) within 30–40 m. Almost all (329 or >99%) twigs were taken from perches at heights of 2–15 m in nest-site habitat (Rosenfield and Bielefeldt, unpubl. data) where canopy trees were about 21 m tall. Hawks took twigs from white and red pine (*Pinus strobus, P. resinosa*), oaks (*Quercus* spp.), black cherry (*Prunus serotina*), black locust (*Robinia pseudoacacia*), box elder (*Acer negundo*), and probably other tree species. It seemed that the hawks were choosing convenient spots near the nest to collect twigs from an abundant supply of building materials.

Breeding Cooper's Hawks in Wisconsin typically build more than one nest during the same year prior to incubation. At least 14 of 16 (88%) and six of 10 (60%) pairs built at least two nests prior to egg laying during 1988 and 1989, respectively. One of these pairs built three nests, and one pair built four nests. Building probably occurred at more than one nest during the same day at five different nesting areas. After two males and one female (from three separate pairs) had collected a twig, they flew out of view instead of flying to the nest under observation. Their mates followed in the direction in which we subsequently found an alternate nest. In two other observation periods, birds left the original site with twigs and probably built on an alternate site, but then returned about 30 min later and resumed building on the original structure. Maximum distances between initial and alternate nests for the 20 pairs ranged from 27 to 335 m ($\bar{x}$ = 170 m).

The need to assure paternity exists in Cooper's Hawks, as in other species with biparental care, because cuckolded males raising unrelated young would waste reproductive investment and lose individual fitness (Trivers 1972). Male Cooper's Hawks do most of the food-provisioning for their mates during the prezygotic period, hunt for prey away from the nest site, and thus must leave females unattended for parts of the day. Unattended females could be inseminated by other males. Moreover, females certainly do no know when, or if, resident males will return with food or return at all. Copulations are associated with prey deliveries. It might be advantageous for females to accept or even solicit extra-pair copulations (EPCs) in return for prey surrendered by non-resident males as a means of maximizing energy assimilation for egg production. Although no one has observed EPCs in Cooper's Hawks, several aspects of the males' behavior suggest that EPCs do occur. The copulation frequency of Cooper's Hawks was high, with an estimated average of 372 copulations in the 30-day period prior to egg laying; frequent copulations may help to assure paternity as suggested for other falconiforms (Birkhead et al. 1987). Among falconiforms, copulation rates are positively correlated with the extent of the male's provisioning of the mate (Moller 1987). Male Cooper's Hawks exhibit high paternal investment through courtship feeding, and as a result they should also invest heavily in paternity assurance (Birkhead and Lessells 1988).

Nest building—a related way to seek to assure paternity—and copulatory behavior are linked to each other by the timing of copulations, 70% of which immediately followed nest visits by males. It may be that nest visits by the male function as a pre-coital display that induces females to copulate and alternate nests may simply serve as another display site. Copulations occurred over a four week period prior to egg laying. It might be to the female's benefit to conceal her fertile period and solicit copulations before she is fertile to induce courtship feeding or nest building from the male (Birkhead and Lessells 1988). Cooper's Hawks may seek to assure paternity by remaining near the nest and the female (i.e., mate guarding; Parker 1974). Males need not leave the immediate vicinity of the nest for building materials because an abundant supply exists within 80 m of the nest. Although males did not hunt at the nest site they nevertheless were present at the nest for a large part of the day.

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The voice and first nesting records of the Zigzag Heron in Ecuador.—Recent sightings of the little-known Zigzag Heron (*Zebrilus undulatus*) have come primarily from Peru, as reported by Mathews and Brooke (Wilson Bull., 100:147–148, 1988) and by Davis et al. (Condor, 82:460–461, 1980). Neither Hilty and Brown (A Guide to the Birds of Colombia, Princeton Univ. Press, 1986, p. 68) nor Hancock and Kushlan (The Herons Handbook, Harper and Row, New York, 1984, pp. 230–232) mention any recorded nests of this species. Here we report on five nests that we found at La Selva Lodge (00°24′S, 76°39′W), approximately 100 km by river down the Napo River (Río Napo) from the town of Coca, Napo Province, Ecuador, elevation 280 m.

La Selva Lodge is located in an area of undisturbed lowland rainforest on the north bank of the Napo River. There are two oxbow lakes with substantial lakeside vegetation separated by 1 km of rarely flooded upper *varzea*. One of the lakes, Garzacocha, is dominated by overhanging trees and drains into *Heliconia*-dominated *varzea*. The other lake, Mandicocha, is dominated by *manglar* trees (*Coussapoa trinervia*, Moraceae) and is connected to the Napo by two flowing streams, one at each end. Sightings of Zigzag Herons in this area have become quite frequent in recent years, with both adults and immatures found calling at dawn and dusk. These individuals prefer the edges of oxbow lakes thick with low fringing vegetation, especially fallen trees at the water's edge, and that are surrounded by undisturbed forest.

Paul Greenfield (pers. comm.) recorded the first call of the Zigzag Heron; it resembles the "oooop" call of the Fulvous-bellied Antpitta (*Hylopezus fulviventris*) when given in a series. This call can also be described as a hollow hooting, sometimes given alone, and sometimes given in a series of 7 or 8 calls at a rate of one/sec. A second call is a nasal, higher-pitched "ahnnn" that is delivered singly. A third call combines vocal characteristics of the first two calls and is given in a series. Only adult herons have been observed giving the hooting call, and juveniles most frequently have been observed giving the "ahnnn" call but respond aggressively to both calls. Adults and juveniles appear to be equally responsive to playback calls from a tape recorder. On one occasion, a juvenile plumaged individual was seen giving the hooting call, but the possibility still exists that the different calls are related to maturity. Both adults and juveniles deliver their calls with the bill tipped slightly upward and the mandibles slightly apart; the throat can be seen moving as the sound is produced.

Nest records from two years of observation at this locality (see Table 1) suggest that the Zigzag Heron breeds from April through July and that the herons may nest more than one time in one season. The Zigzag Heron appears to lay only one egg, as often reported for the Rufescent Tiger-Heron (*Tigrisoma lineatum*) (Hancock and Kushlan 1984). The Zigzag Heron egg was pure white, rather than the bluish-white, often blotched eggs of the Rufescent Tiger-Heron reported by Hancock and Kushlan (1984). Downy young appear completely yellowish-cream or white and gradually mature into the rufous immature plumage, with the darker feathers of the head, wings, and back emerging last. The bill and legs of the juvenile

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COLOR PLATE

The Zigzag Heron (*Zebrilus undulatus*). This painting by Tracy Pedersen was the George Miksch Sutton Award winner at the Centennial Meeting of The Wilson Ornithological Society in 1988 at Rosemont College, Rosemont, Pennsylvania. This color plate has been made possible by an endowment established by George Miksch Sutton.

TABLE 1
COMPARISON OF ZIGZAG HERON NESTS

Nest	Height above water (m)	Distance from bank (m)	Active dates	Edge-barrier present	Young observed	Egg observed
1	1.5	2.0	30 April–17 May 1989	Yes	Yes	Yes
2	2.0	N/A	29 June–5 July 1989	Yes	Yes	No
3	3.0	2.0	20 May–27 May 1990	Yes	Yes	No
4	1.0	3.0	9 June–12 June 1990	No	No	No
5	1.5	N/A	July 1990	Yes	Yes	No

Zigzag Heron are yellowish-green, whereas the adult has a blackish bill and grayish horn legs. The adults were not seen near the nest as the young grew, and it is assumed that this was due to increased time expenditures on hunting.

The five nests were all shallow, round platforms averaging 17 × 22 cm. They were similar to nests of the larger Rufescent Tiger-Heron nests discovered in the same area, but they were usually ringed by a thorny edge-barrier while the Tiger-Heron nests were not. The edge-barriers were made from various thorny plants, primarily *Uncaria tomentosa* (Rubiaceae), known locally as uña de gato, and *Bactris* palms. The nests were found on the edge of water, either an oxbow lake or a permanent stream. Nests were placed an average of 1.5 m above the water, although up to 3 m above the water when the level was low. When built on a stream edge, nests averaged 2 m from the bank. The one egg discovered was elongated and white.

The first of the five nests was discovered 30 April 1989 and was observed until 17 May 1989. The nest was located approximately 400 m eastward down a small stream, approximately 8 m wide, connecting the eastern edge of the oxbow lake Mandicocha to the Napo River, roughly 1.5 km to the south. The area is often flooded, although the mud banks keep the stream course well defined. The level of the stream fluctuates with the level of the Napo River and is thus dependent on the rainfall in the mountains to the west. The nest was placed midway up a coco palm (*Bactris* sp.) within a patch of extremely thorny chontilla (*Bactris* sp.) fronds. The *Bactris* fronds were woven into the edge of the nest. The nest was within 100 m of a Rufescent Tiger-Heron nest that was located approximately 4 m above the water and centered over the stream.

One adult Zigzag Heron was always present on the nest. The adult's plumage and posture appeared as described in Hilty and Brown (1986), with the adult maintaining the bittern-posture with its head held upright while on the nest.

The nest was viewed from below by canoe, yet the adult nevertheless maintained a vertical posture. The adult always faced towards the viewer and used cautious body movements rather than head movements to maintain eye contact, although occasional slight head rotation was noted. The continuous nervous tail-flicking of foraging birds noted by Mathews and Brooke (1988) was not seen, although occasional slow tail-flicks of this type were noted at the rate of one per 10-min period.

On 7 May 1989, one egg, 4 cm in length, appeared on the nest. The adult and egg were present together until 17 May 1989, when both disappeared. Presumably, the egg loss was due to predation following which the adult abandoned the nest.

A second nest containing one downy young was found 29 June 1989. The nest was

approximately 1 km from the first nest on the incoming, rather than the outgoing, stream connecting the western edge of Mandicocha to the Napo River. Given the distance between the two nests and the relatively high numbers of Zigzag Herons observed in the area, it is unlikely that the second nest was a second nesting attempt by the first pair. The area is a wooded swamp and the nest was located in a manglar tree surrounded by water. This nest resembled the other nests with thorny sticks woven into the outside edge; in this case the thorns were of *Uncaria tomentosa*, portions of fronds of *Bactris* palms, and other thorny plants and vines. This nest was within 30 m of a Hoatzin (*Opisthocomus hoatzin*) nest which was similarly placed over the water.

The young Zigzag Heron was seen on or near the nest until 5 July 1989. This bird differed considerably from the adult and immature plumage descriptions of Hilty and Brown (1986) and was presumably in juvenile plumage. It was approximately 20 cm tall and uniformly yellowish-cream with grayish wings and no trace of rufous. The head had traces of white down and no hint of the blackish adult crest. When viewed from close range, the young heron appeared agitated: it silently moved its head from side to side and hopped from the nest to its supporting branches and back again to the nest, but it never strayed farther than 20–30 cm from the nest.

A third nest (WFVZ #161934) found 20 May 1990 was on the eastern edge of Mandicocha in the same area as the first nest. This nest was again a small platform with *Uncaria tomentosa* woven into the nest as an edge-barrier. This nest was in a small, sparsely branched tree. The nest was collected on 16 August 1990.

When the third nest was discovered, it contained one downy young, with the adult heron perched on a branch approximately 1 m from the nest. The young heron had whitish downy feathers on the head and neck, with the body and wings covered with very lightly colored, rusty feathers. The flight feathers were undeveloped. During this visit, the adult maintained an erect bittern-posture while facing the observer and did not make any discernable movements.

On 24 May 1990, only the young heron was present on the nest. The down feathers remained only on the head, and darker rufous was visible on the face and back. The bill and legs were yellowish-green, and the iris was bright yellow.

This juvenile was last seen at the nest 27 May 1990, approximately 1 m from the nest on supporting branches. No down remained on it, and the plumage closely resembled the immature plumage pictured in Hancock and Kushlan (1984) and described in Hilty and Brown (1986), but without the rufous chestnut breast.

The fourth nest was found on 9 June 1990, again on the eastern extension of Mandicocha, approximately 100 m eastward down the stream from the lake. It is possible, given the proximity of the third and fourth nests, that these were by the same nesting pair. The nest was in a low overhanging bush.

When the nest was discovered, it was occupied by one adult heron. No egg or young was ever seen on this nest. On 12 June 1990, the nest was washed away by an exceptionally high flood several meters higher than any reported in the two years that the stream has been informally monitored.

The fifth nest was found in early July in a small tree (*Inga* sp., Mimosaceae) on the edge of an inlet to the *varzea* waterway system of Garzacocha, on the southeastern edge of the lake. Garzacocha is not connected to the Napo River by streams as is Mandicocha, but rather is connected by frequently inundated *varzea* for the 0.5 km to the river. Garzacocha is completely surrounded by primary forest except for a small clearing around the lodge compound. The edge of the lake on the eastern side is dominated by *Heliconia* sp. with sparsely distributed *Coussapoa trinervia* and other small trees. The nest tree was roughly 1 m from the open water of the lake. Little information was gathered on this nest, although

the adult heron was frequently seen on the nest, and later a juvenile was sighted near the nest.

Although sightings are most frequent on the edges of the oxbow lakes, several individuals have been seen in a single day in the 1 km of rarely flooded upper *varzea* forest separating the two lakes (Paul Coopmans, pers. comm.). We suggest that the Zigzag Heron may prove to be more numerous than previously thought in areas that provide the proper requirements. Among these requirements may be a closely related series of oxbow lakes with substantial lakeside vegetation and undisturbed forest. The frequency of sightings in such habitat at La Selva Lodge suggests that the paucity of past sightings may be a result of the secretive habits, previously unknown voice, and the specific habitat requirements of the Zigzag Heron, rather than uniformly low population numbers throughout its range. Given the knowledge of these specific habitat requirements and its voice, Zigzag Herons may be found to range widely but thinly throughout Amazonia and the Guianas.

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Enhanced fledging success by colonially nesting Ospreys in Nova Scotia coastal habitat.—Historically, Ospreys (*Pandion haliaetus*) often nested in colonies along the Atlantic coast of North America. One colony on Gardiner's Island, New York, contained as many as 300 pairs in the early 1900s (Puleston 1977). Recently, more colonial nesting has been reported (e.g., Spitzer and Poole 1980, Hagan and Walters 1990). In Nova Scotia, colonies have been reported by Prévost et al. (1978) and by Greene (1987); the former was part of the population examined in the present study.

An Osprey colony could function as a center where flock mates are obtained for the purpose of social foraging (Flemming 1988, Hagan and Walters 1990). Flemming (1988) found that social foraging reduced the time required to locate prey. This suggests that colonial Ospreys might provide more food to their young, thereby enhancing the adult's reproductive success. The objective of this study was to determine if colonial Ospreys fledged more young than those nesting solitarily and, furthermore, to test whether this was related to colonial nesting alone rather than to nesting habitats or types of nest sites.

Study area and methods.—We studied Ospreys in northeastern Nova Scotia primarily within the Pomquet, Antigonish, and Pictou Harbour watersheds. Each of these watersheds flows into one of several shallow estuaries that border the coastline of the Northumberland Strait. The highlands are covered with deciduous and mixed forests, while valley slopes and poorly drained areas are dominated by coniferous forest. Harvesting of coniferous stands is extensive. Several powerline corridors bisect the study area. Pairs were considered to be nesting along the coast if their nest sites were within 6 km of an estuary, where most coastal foraging by Ospreys occurs (Jamieson et al. 1982). The next closest Ospreys were a distant

13 km from the coast, and were considered inland nesters because their primary foraging sites were inland rivers and lakes (Jamieson et al. 1982). Most nests (70%, N = 188) were in the coastal zone. Seventy-nine percent (N = 131) of coastal Ospreys nested on utility poles, while only half (47%, N = 57) of inland pairs used utility poles as nest sites. Many (31%, N = 188) pairs used more widely dispersed natural nest sites.

Osprey nests were located by land search and from aircraft. Surveys by helicopter enabled us to assess whether an Osprey nest was occupied and active and allowed us to determine the pair's clutch size and fledging success. During the period of 25 May–3 June of 1976, 1978, 1979, 1980, 1981, and 1985, a combined nest occupancy, nest activity, and clutch size survey was conducted for a total of 188 nests. During the 1985 census, nest distribution and inter-nest visibility were also noted. A nest was considered occupied if it was attended by one or more birds (cf. Postupalsky 1974), and it was considered active if it had at least one egg. Fledging success surveys were undertaken during the period of 21–26 July of the same years. Helicopter surveys conducted later than this risk causing premature fledging. All but six nests were revisited, resulting in data for 182 nests. Since this survey period was late in the nestling phase, we assumed that nestlings alive at that time would fledge successfully.

Nearest-neighbor distances between nests and nest-to-estuary distances were normally distributed, so Student's *t*-test was used to test for differences. Clutch size and fledging success data were not distributed normally, so non-parametric statistics were employed. The Kruskal-Wallis test was used to determine if clutch size or fledging success varied with census year. The *G*-test of independence was used to test whether or not nesting status was independent of eggs/fledglings produced each year. Analyses followed methods described in Zar (1984).

Results.—The mean distance (1985) between nearest neighbors using utility poles as nest sites (occupied) in coastal habitat was 0.7 ± 1.1 km (mean ± SD, N = 33). However, it was 6.7 ± 6.2 km (N = 25) between all other nests used by Ospreys. These distances were significantly different (Student's *t*-test, $P = 0.02$), suggesting that coastal Ospreys using utility poles nested in the highest density in our study area. When perched near their nests, most (80.6%, N = 31) coastal Ospreys nesting on utility poles had unobstructed views of 4–9 other nests. The maximum distance between extreme nests in these groups was 2.2 km. Moreover, by flying above their nests, all other pairs could see at least two nests along these straight powerline corridors. Therefore, although there was some variation in inter-nest visibility, all coastal pairs using utility poles as nest sites could readily observe and interact with their neighbors and hence were considered colonial.

In the coastal habitat, occupied colonial nests on utility poles were an average of 2.8 ± 1.7 km (N = 33) from the closest estuary to each nest, while Ospreys nesting solitarily on natural nest sites were an average of 2.4 ± 1.5 km (N = 10) from the closest estuary. The distance from nests to estuaries was not significantly different between these two groups (Students *t*-test, $P = 0.50$), suggesting that neither group had an advantage in terms of proximity to an estuary.

Clutch size did not vary significantly from year to year (Kruskal-Wallis test) for either occupied ($P = 0.14$) or active nests ($P = 0.45$), so the data were pooled for further analysis (Table 1). There was no significant difference in clutch size between birds nesting in coastal (2.09 eggs/occupied nest, 2.56 eggs/active nest) and inland (2.40, 2.74) habitats (*G*-test of independence, $P = 0.29$, $P = 0.27$). There was also no significant difference (*G*-test, $P = 0.47$, $P = 0.31$) in clutch size between pairs nesting colonially on coastal utility poles (2.09, 2.56) versus those nesting solitarily on coastal natural nest sites (2.11, 2.57). Finally, clutch size for inland solitary nesting Ospreys using utility pole (2.30, 2.58) and natural sites (2.50, 2.89) was not significantly different (*G*-test, $P = 0.63$, $P = 0.47$).

Table 1

Comparison of Clutch Sizes between Ospreys Nesting in Coastal Versus Inland Habitat, and between Coastal and Inland Ospreys Nesting on Utility Poles vs Natural Sites

Comparison	Occupied nests	Active nests	Eggs	Clutch size/ occupied nest[a]	Clutch size/ active nest[a]
Coastal	131	107	274	2.09 ± 1.21[b]	2.56 ± 0.76[b]
Inland	57	50	137	2.40 ± 1.11	2.74 ± 0.69
Coastal utility pole (colonial)	103	84	215	2.09 ± 1.22[b]	2.56 ± 0.78[b]
Coastal natural site (solitary)	28	23	59	2.11 ± 1.17	2.57 ± 0.66
Inland utility pole (solitary)	27	24	62	2.30 ± 1.10[b]	2.58 ± 0.78[b]
Inland natural site (solitary)	30	26	75	2.50 ± 1.14	2.89 ± 0.59

[a] Mean ± SD.
[b] Compared are not significantly different ($P > 0.05$).

As with clutch size, fledging success per occupied and per active nest did not vary from year to year (Kruskal-Wallis test, $P = 0.30$, $P = 0.23$), hence the data were pooled (Table 2). The number of young fledged per occupied nest and per active nest was significantly greater (G-test, $P = 0.02$, $P = 0.01$) for the coastal habitat (1.50 fledglings/occupied nest, 1.80 fledglings/active nest) than for the inland (1.16, 1.32) habitat. Similarly, for the coastal habitat, there was a significant ($P = 0.03$, $P = 0.04$) difference when the same test was used to determine whether or not colonial utility pole nesters (1.53, 1.86) fledged more young/nest than pairs nesting solitarily on natural sites (1.40, 1.59).

If the type of nest (utility pole vs natural) site influenced fledging success, this should have occurred in both coastal and inland habitats (Table 2). However, there was no significant difference (G-test, $P = 0.32$, $P = 0.28$) in young fledged by inland nesting Ospreys that used utility poles (1.24, 1.36) versus those that used natural sites (1.07, 1.26).

Discussion.—Greene (1987) reported that Osprey colonies functioned as a center where colony members could obtain information from one another about the location of distant food sources (cf. Ward and Zahavi 1973). However, Hagan and Walters (1990) found no evidence of information transfer in a North Carolina colony. They suggested that Greene's (1987) findings may have been due to local enhancement. This explains much of the data (Flemming and Greene 1990). An animal foraging by local enhancement joins one or more conspecifics that have indicated in some manner that that have located prey. As a result the animal finds food more readily (Thorpe 1963).

Flemming (1988) and Hagan and Walters (1990) reported flocks forming at colonies. Flemming (1988) also reported that Ospreys used several social foraging strategies, including local enhancement. This resulted in reduced time required to locate prey. It seems reasonable that being part of a colony could facilitate obtaining conspecifics for social foraging (cf. Evans 1982), and this could be one of the benefits obtained by Ospreys nesting in colonies.

If foraging advantages accrue to Ospreys nesting in colonies, this presumably should be reflected in enhanced reproductive success. These benefits would most likely be seen in terms of fledglings produced, rather than eggs produced, since Poole (1985) showed that clutch size was not correlated with pre-laying feedings rates. Clutch size in this study did not vary with habitat or with nesting site regardless of habitat.

Fledging success was greater for Ospreys nesting in the coastal habitat than inland. How-

TABLE 2

COMPARISON OF FLEDGING SUCCESS BETWEEN OSPREYS NESTING IN COASTAL VS INLAND HABITAT, AND BETWEEN COASTAL AND INLAND OSPREYS NESTING ON UTILITY POLES VS NATURAL SITES

Comparison	Occupied nests	Active nests	Fledglings	Fledging succ./ occupied nest[a]	Fledging succ./ active nest[a]
Coastal	121	101	182	1.50 ± 1.19[b]	1.80 ± 1.08[b]
Inland	61	54	71	1.16 ± 1.20	1.32 ± 1.20
Coastal utility pole (colonial)	96	79	147	1.53 ± 1.26[b]	1.86 ± 1.14[b]
Coastal natural site (solitary)	25	22	35	1.40 ± 0.91	1.59 ± 0.80
Inland utility pole (solitary)	34	31	42	1.24 ± 1.26[c]	1.36 ± 1.25[c]
Inland natural site (solitary)	27	23	29	1.07 ± 1.14	1.26 ± 1.14

[a] Mean ± SD.
[b] Compared are significantly different ($P < 0.05$).
[c] Compared are not significantly different ($P > 0.05$).

ever, the fledging success of coastal pairs nesting colonially on utility poles was higher than for those nesting solitarily on natural sites, even though solitary nesters were as close to estuarine foraging areas as colonial birds. Therefore, habitat was not solely responsible for the observed differences in fledging success, as it does not explain the latter finding.

That the type of nest site was responsible for the variation in fledging success is also an unsatisfactory explanation of our results. While utility pole nesters fledged more young than birds using natural sites in the coastal habitat, fledging success did not differ between birds using these two types of nest sites in the inland habitat.

The enhanced reproductive success of coastal Ospreys nesting on utility poles seems related to another factor. In coastal habitat, the only apparent behavioral variable related to the provisioning of food to nestlings that distinguished solitary natural site nesters and colonial utility pole nesters was the recruitment of flock mates at the colony for social foraging. It appears likely that enhanced opportunities for social foraging by colonially nesting Ospreys can result in a greater number of young fledged.

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The avifauna of the Revillagigedo Islands, Mexico: additional data and observations.—The Revillagigedo Islands are an archipelago of four oceanic volcanic islands in the eastern Pacific Ocean about 650 km (400 nautical miles) west of the Mexican state of Colima. Clarión (3.5 × 8.5 km) is the westernmost and oldest island (early Pliocene). Roca Partida is a rocky islet and is the throat of an old volcano. It is younger than Clarión but older than Socorro, the largest island (16.5 × 11.5 km, early Pleistocene), and San Benedicto (4.5 × 0.9 km), the youngest and northernmost island (late Pleistocene). Seabirds are numerous and diverse, but include only one endemic species. The terrestrial avifauna is relatively depauperate, but its degree of endemism is very high. Socorro, the largest and most diverse island, has the largest number of endemic land birds, followed by Clarión, the second largest but oldest island. The smallest, Roca Partida, has none, and the second smallest and youngest island, San Benedicto, had only one, a Rock Wren (*Salpinctes obsoletus exsul*), that became extinct following the catastrophic volcanic eruption in 1952 (Brattstrom 1990).

Numerous visitors have discussed the status of birds of the Revillagigedos including Grayson (1872), Anthony (1898), Brattstrom and Howell (1956), Jehl and Parkes (1982), Everett (1988), and Howell and Webb (1990). We conducted a cruise in the area from 29 April to 8 May, 1990, visiting all four islands as follows: San Benedicto (19°18′N, 110°49′W) 29–30 April; Socorro (18°47′N, 110°58′W) 30 April–3 May; Roca Partida (19°00′N, 112°04′W) 4 May; and Clarión (18°22′N, 114°45′W) 5–7 May. While at sea, we maintained a continuous watch for seabirds. We here add recent data to the status of the known avifauna of the Revillagigedo Islands and include our observations of other species never observed before on or around the islands.

San Benedicto remains uninhabited, and we saw no land birds or introduced species. Because of rough seas, we could not land on the northern part of the island, which seabirds successfully recolonized after the devastating volcanic eruption of 1952 and where nesting was observed by Howell and Webb (1990). We circled the island, and seabirds were abundant over and all around it. We were able to land on the southeastern part, where lava and ash cover practically everything. Seabirds, except for roosting boobies and airborne frigatebirds, were few.

Socorro has a Mexican naval garrison that has grown to 250 people, including women and children. Introduced sheep are abundant (greater than 3000 animals) and are hunted by the garrison (only young males are taken). The resulting overpopulation of sheep has degraded the landscape, caused severe erosion in areas, and prevented regeneration of many of the forests. This further endangered the endemic avifauna, especially the highly endangered Socorro Mockingbird (*Mimodes graysoni*). Feral cats are seen infrequently (we saw none), and their population is unknown, but they may be responsible for the extirpation of the Socorro Dove (*Zenaida graysoni*), the near-extinction of the Socorro Mockingbird, and the disruption of the breeding colonies of Townsend's Shearwater (*Puffinus auricularis*) (Jehl and Parkes 1982, 1983; Parkes 1990). There is an effort underway to eliminate the cats. We spent 1½ days on Socorro, traveling by truck from the garrison via the landing strip to the base of Cerro Evermann. From there we proceeded on foot on 2 May to the wooded areas where the Socorro Mockingbird was found in 1990 by Mexican observers, and thence to the top of the volcano (1130 m) where we saw no evidence of nesting seabirds in areas where Townsend's Shearwater historically had nested. (McLellan 1926, Jehl and Parkes 1982).

Clarión has a naval garrison of nine men who live under rather difficult conditions. The introduced feral rabbits and pigs, a food source for the garrison, have damaged the ecology of the island. The rabbits appear to have occupied practically all seabird burrows, and the pigs virtually have destroyed all the prickly pear cactus (*Opuntia* sp.) on the island. They are now starting to root and destroy the small trees and large bushes on which the Red-footed Booby (*Sula sula*) nests. Goats have also been recently introduced. Sheep now number about twenty and are protected from hunting until their numbers increase further. Data gathered by our expedition have been forwarded to the proper officials in Mexico City, where there is genuine concern for the conservation of Clarión as well as Socorro.

The following list summarizes our observations; * indicates the species has not been recorded previously in the Revillagigedo Islands.

* Short-tailed Albatross (*Diomedea albatrus*).—We saw one adult on 29 April flying low over the water at 19°26′N, 110°44′W, 10 km (six nautical miles) north of San Benedicto (Santaella and Sada, in press). As far as we are aware, this is the first record for the Revillagigedo Islands and only the second this century for Mexico (L. Spear, pers. comm.).

Laysan Albatross (*D. immutabilis*).—We saw two on 29 April flying at 19°32′N, 110°43′W, about 10.5 km (6.5 nautical miles) north of San Benedicto and one on 4 May flying past Roca Partida. Four birds were present on the ground at Clarión, 5–6 May, near the naval station. These were remarkably tame, and one pair demonstrated courtship ritual, but we found no evidence of nesting. Members of the naval garrison assured us that there had been many more albatrosses earlier in the year. Since Howell and Webb (1990) reported much larger numbers in February, May is apparently late in the season for this species on Clarión.

* Juan Fernández Petrel (*Pterodroma externa*).—On 7–8 May we observed about 70 petrels 30–260 km (19 to 150 nautical miles) northeast of Clarión, both flying and rafting, the largest raft numbering approximately 40 birds. Previously only Pitman (1986) had reported this petrel from Mexican waters, but he believes that it is the commonest *Pterodroma* off western Mexico and that most individuals are non-breeders found nearly year-round (Pitman, pers. comm.).

* Tahiti Petrel (*P. rostrata*).—We saw one on 8 May gliding and banking over the water at 20°13′N, 112°41′W, 170 nautical miles northeast of Clarión. Again, only Pitman (1986) had reported this petrel from anywhere in Mexican waters.

* Cook's Petrel (*P. cookii*).—This petrel has been regularly recorded off Baja California (Wilbur 1987) and off western Mexico (Pitman 1986). We saw three on 29 April at 19°57′N, 110°37′W, north of San Benedicto, one at 19°00′N, 112°06′W on 4 May between Roca Partida and Clarión, and six on 7–8 May up to 170 nautical miles northeast of Clarión.

* Black-winged Petrel (*P. nigripennis*).—We observed one on 7 May at 18°34′N, 114°27′W, 19 nautical miles northeast of Clarión. Pitman (1986) has reported this petrel off Western Mexico.

* Flesh-footed Shearwater (*Puffinus carneipes*).—We observed two individuals: one on 4 May between Roca Partida and Clarión and the other on 7 May northeast of Clarión.

Wedge-tailed Shearwater (*P. pacificus*).—We observed several hundred around San Benedicto on 29 April, where they are known to breed (Brattstrom and Howell 1956, Jehl and Parkes 1982), the most northerly sighting being at 19°41′N, 110°39′W. The proportion of dark to light morph birds was approximately 60% to 40%. We saw these shearwaters flying at dusk and early evening, over the boat, directly to the northern part of the island, where presumably their nests were located. On 30 April, we observed 25 between San Benedicto and Socorro. From 1 to 7 May we saw another 10 around Socorro and Roca Partida, between the latter and Clarión, and all around Clarión. We found no evidence of nesting on either Socorro or Clarión. No shearwaters of this species were observed by Howell and Webb (1990) in February.

Townsend's Shearwater (*P. auricularis*).—Our first sighting was of two birds on 29 April at 20°28′N, 110°30′W, approximately 40 nautical miles north of San Benedicto, while still out of sight of land. From there until arrival at San Benedicto, we saw four more. Between 20:00 and 21:30 h that evening, we observed approximately 20 of these shearwaters flying over the boat directly to the northern part of the island, just as the Wedge-tailed Shearwaters were doing. This observation suggests possible recolonization by this shearwater at San Benedicto, the first evidence since the volcanic eruption of 1952. On 30 April, we saw three birds between San Benedicto and Socorro. We found no direct evidence of breeding by this highly endangered endemic species on Socorro, although very recently three nesting colonies have been found on the northern part of the island (A. Castellanos, pers. comm.). Jehl (1982) estimated the Socorro breeding population at 1000 pairs, but Howell and Webb (1990) did not report any breeding there. On 4 May, we saw only one bird between Roca Partida and Clarión. On Clarión, Everett (1988) found no occupied burrows in January, and Howell and Webb (1990) found all nesting sites marked by severe pig rooting, and numerous shearwater remains littered the destroyed burrows. They found no occupied burrows. Several members of our expedition spent the night of 5 May on Clarión, exploring the little-known eastern end and found no evidence of recent nesting or of shearwaters coming to land. We all explored on 5–6 May the western and central portions of the island. All burrows found were old and occupied by rabbits or destroyed by pigs. We found neither bones nor feathers and saw only five birds flying over the boat at night in the direction of land. Between 4 and 7 May we saw only six others in Clarión waters. It appears that this shearwater may have all but abandoned Clarión, its former stronghold (McLellan 1926).

* Audubon's Shearwater (*P. lherminieri*).—This shearwater has never been recorded as far north as the Revillagigedo Islands and usually is encountered only in the eastern Pacific from Acapulco south (R. Pitman, pers. comm.). Six birds were seen on 29 April at 20°26′N, 110°29′W, about 60 km (35 nautical miles) north of San Benedicto, where the water had suddenly changed from 70° to 78°F. We saw ten on the same day en route to and around San Benedicto and 110 between San Benedicto and Socorro on 30 April. We found this

bird nowhere else in the Revillagigedos. The smaller size, brown extending below the eye and as a half moon on the sides of the neck, and lack of white flanks readily differentiated Audubon's Shearwaters from the Townsend's Shearwaters that often accompanied them.

* Wilson's Storm-Petrel (*Oceanites oceanicus*).—This species has been recorded only occasionally off western Mexico (Pitman 1986) and never in the Revillagigedo Islands. We saw two on 29 April at 20°07′N, 110°35′W, north of San Benedicto, two off Roca Partida on 4 May, and one off Clarión on 7 May.

Leach's Storm-Petrel (*Oceanodroma leucorhoa*).—The nearest known breeding colonies of this storm-petrel to the Revillagigedo Islands are on islands off the Pacific Coast of Baja California. Wintering birds are regularly found off western Mexico and among the Revillagigedos (Pitman 1986). We observed about 15 birds throughout the archipelago. All were white-rumped, except for one entirely dark-rumped and one other partially so.

* Band-rumped Storm-Petrel (*O. castro*).—This storm-petrel has been observed infrequently off western Mexico (Pitman 1986). On 29 April, we observed one at 20°20′N, 110°31′W and three at 19°57′N, 110°37′W, north of San Benedicto and on 7 May, two northeast of Clarión.

* Wedge-rumped Storm-Petrel (*O. tethys*).—This species is common off western Mexico (Pitman 1986) and although not reported previously, it is the most abundant storm-petrel in the Revillagigedo Islands, in our experience. We saw 230 birds throughout the archipelago, the most (150) on 4 May around Roca Partida.

Black Storm-Petrel (*O. melania*).—Three of these storm-petrels followed our boat from shortly after departure from Cabo San Lucas on 28 April until 29 April, when at 20°26′N, 110°29′W, north of San Benedicto, where the water temperature suddenly changed from 70° to 78°F, the birds abruptly departed. We saw no others anywhere in the archipelago.

Red-billed Tropicbird (*Phaethon aethereus*).—We saw 50 around San Benedicto, mostly about the northern cliffs; 12 along the cliffs at Cabo Pearce, Socorro, on 3 May; and another 24 around Clarión, mainly off the northwestern and eastern cliffs.

Red-tailed Tropicbird (*P. rubricauda*).—One flew over our boat on 29 April about 8 km (5 nautical miles) north of San Benedicto, and another landed on a ledge on a cliff on the northwestern side of the island. Rough seas prevented a close approach to detect whether the bird was nesting.

Masked Booby (*Sula dactylatra*).—We saw at least 300, including many juveniles, around San Benedicto on 29–30 April and 10 between San Benedicto and Socorro on 30 April. All were the yellow-billed form, *S. d. californica*. On 4 May, we saw 50 roosting adults on Roca Partida, among which were three pairs of *S. d. granti*, the distinctive orange-billed Galápagos form. Two of the pairs were displaying and could have been nesting on ledges of the south pinnacle. At most 100 pairs of *S. d. californica* were nesting on the ground at two sites on the western end of Clarión. All were on eggs or had very young chicks. This number is lower than that found by Howell and Webb (1990). Despite previous reports (McLellan 1926, Brattstrom and Howell 1956), no one has seen the Blue-footed Booby (*Sula nebouxii*) on or near the Revillagigedo Islands in recent years.

Brown booby (*S. leucogaster*).—We observed no more than ten, mostly adults, around San Benedicto. Since Howell and Webb (1990) observed many more and confirmed breeding in February, our low number suggests fledgling dispersal after breeding. On 1 May, we saw 30 birds roosting on the cliffs of Cabo Henslow, Socorro. Over 100 were present on Roca Partida on 4 May. On Clarión, we saw eight around the island but none on land. Howell and Webb (1990) also saw very few at Clarión.

Red-footed Booby (*S. sula*).—We found few (<15), mostly juveniles, around San Benedicto and Socorro. On 4 May between Roca Partida and Clarión, we observed several adults swooping for flying fish disturbed by our boat. We found 3000 pairs nesting on small trees

and large bushes at five sites, all on the eastern half of Clarión. Practically all nests had down-covered chicks. The birds were very tame and appeared to ignore our presence. Most (99%) adults were white morphs. Of the white morphs, 80% were black-tailed and 20% were white-tailed.

Magnificent Frigatebird (*Fregata magnificens*).—We saw six around San Benedicto, another six around Socorro, possibly one off Roca Partida, and none on Clarión. This frigatebird apparently does not reach Clarión (Everett and Anderson, in press).

Great Frigatebird (*F. minor*).—This frigatebird appears to greatly outnumber *F. magnificens* in the Revillagigedo Islands (Howell and Webb 1990). We saw at least 100, mostly females and juveniles about or around San Benedicto on 29–30 April; none on Socorro; two or three around Roca Partida on 4 May; and twelve around Clarión, including three or four daily at Sulphur Bay between 5 and 7 May. We found no evidence of nesting either on Roca Partida or Clarión.

Great Blue Heron (*Ardea herodias*).—We saw two at Bahia Braithwaite, Socorro, on 2–3 May and one on Clarión on 5 May.

Cattle Egret (*Bubulcus ibis*).—Although recorded from Socorro (Jehl and Parkes 1982), there appear to be no previous records from Clarión. We saw one in the twin canyon area, close to the Red-footed Booby colonies in the interior of Clarión.

Socorro Red-tailed Hawk (*Buteo jamaicensis socorroensis*).—We encountered four individuals of this endemic subspecies 2–3 May. Two were near the summit of Cerro Evermann. Unlike most of the endemic landbirds, this hawk was wary and did not permit close approach.

Pacific Golden Plover (*Pluvialis fulva*).—We saw two in basic plumage on 6 May on the grassy plateau in the center of Clarión. This species is considered accidental on Clarión (Brattstrom and Howell 1956) but may actually be regular on the islands (Howell and Webb 1988).

Wandering Tattler (*Heteroscelus incanus*).—We saw one on rocks at Caleta Trueno, northwest Socorro, on 1 May and three on rocks in Sulphur Bay, Clarión, on 7 May.

Spotted Sandpiper (*Actitis macularia*).—We saw one on rocks at Cabo Henslow, Socorro, on 1 May and another on rocks at Sulpher Bay, Clarión, on 7 May.

Whimbrel (*Numenius phaeopus*).—We saw one at Bahia Braithwaite, Socorro, on 2 May and two at Sulphur Bay, Clarión, on 5 May.

California Gull (*Larus californicus*).—We observed two juveniles on the southeastern beach of San Benedicto on 30 April. These were the only gulls seen in the archipelago.

* Arctic Tern (*Sterna paradisaea*).—We saw five terns fly past Roca Partida on 4 May and one northeast of Clarión on 7 May. All were in full adult breeding plumage with deep red bill, uniformly gray upperwings, and translucent flight feathers.

Sooty Tern (*S. fuscata*).—Over 100 terns were seen on or around O'Neal Rock, off Socorro, on 30 April, and many were nesting. At least another 100 were on Roca Partida on 4 May, some of which appeared to be nesting.

Brown Noddy (*Anous stolidus*).—Over 100 were seen on or around O'Neal Rock and another 50 on Roca Partida, nesting on both rocks.

Mourning Dove (*Zenaida macroura*).—This species is a recent colonizer of Socorro and appears to be *Z. m. marginella* from the Mexican mainland (Jehl and Parkes 1983). It was very common in open and lightly wooded country. The birds were very wary. On the contrary, the very distinct endemic dove of Clarión, *Z. m. clarionensis,* was very tame and allowed close approach. We found it common throughout the island and especially around the naval station where it came to drink. We observed at least 150 birds, in marked contrast to Everett (1988) who noted only 20 individuals.

Socorro Common Ground-Dove (*Columbina passerina socorroensis*).—This endemic subspecies was common in open country on Socorro but did not allow very close approach.

Socorro Green Parakeet (*Aratinga holochlora brevipes*).—We found this endemic subspe-

cies in wooded areas around the slopes of Cerro Evermann. We encountered three flocks of 15, 25, and 10 birds, respectively.

Clarión Burrowing Owl (*Athene cunicularia rostrata*).—We observed about 20 individuals of this endemic subspecies mostly in the higher parts of Clarión, a number greater than Everett's (1988). They were usually seen in daylight, standing beside their burrow, and were very tame. Often the burrows were underneath the small trees where Red-footed Boobies nested.

Chaetura sp.—We observed one small swift flying over the hill in back of the naval station on Clarión on 6 May. *Chaetura* swifts have not been reported previously in these islands.

Barn Swallow (*Hirundo rustica*).—We observed two flying about and perching on wires by the naval station on Clarión on 6 May.

Common Raven (*Corvus corax clarionensis*).—This wary Clarión resident was common all over the island. We also frequently observed ravens perched around the colonies of Red-footed Booby, probably waiting for opportunities to steal eggs and chicks.

Socorro Wren (*Thryomanes sissonii*).—This tame endemic wren was the second most common land bird and was found in both open and wooded areas of Socorro at all elevations.

Clarión Island Wren (*Troglodytes tanneri*).—This endemic wren was common throughout Clarión (at least 100 seen), ranging from the rocks on the beach to the shrubs at the highest elevations. Everett (1988) saw only 20 individuals. They were often observed near the shore in the vicinity of the endemic Clarión snake (*Masticophis anthonyi*), but we saw no interaction between the two species. The few derelict vehicles remaining on Clarión all had nests of this species in the radiator or glove compartment! We noted some plumage variation: some of the wrens found in beach areas were paler and buffier than those found in the vegetation of highland areas.

Northern Mockingbird (*Mimus polyglottos*).—A recent invader (Jehl and Parkes 1982, 1983) that was very common throughout both open and wooded areas of Socorro and behaved exactly like its congeners on the mainland.

Socorro Mockingbird (*Mimodes graysoni*).—This monotypic endemic genus is unique to Socorro. Its affinities with mainland genera are obscure (Gulledge 1975). The Socorro Mockingbird is tame, bold, omnivorous (we witnessed it feeding on young leaves, fruit, large insects, and dead land crabs), and aggressive. It likely is a predator of eggs and nestlings of small passerines (Parkes 1990). Both the endemic Socorro Wren and Tropical Parula Warbler appear to be much more common now that *Mimodes* is nearly extinct (Brattstrom and Howell 1956, Parkes 1990).

From being the most abundant and widespread species of land bird on Socorro (McLellan 1926), *Mimodes* has declined to near extinction, most likely due to the depredations of feral cats (Jehl and Parkes 1982, 1983). In 1978, Jehl and Parkes (1982) found only a few *Mimodes*, mainly in the vicinity of large fig groves (*Ficus cotonifolia*) near the coast. In 1981, the same observers declared the species virtually extirpated. However, in August 1987, 20 individuals were found in a relatively inaccessible part of the island by a party from the Univ. of Mexico (Parkes 1990), and in early 1990 16 were found by a group from the Centro de Investigaciones Biológicas (C.I.B.) of La Paz, B.C.S. (H. Walter, pers. comm.). Following their instructions, we found a family of four *Mimodes* at about 600 m elevation on the way to the summit of Cerro Evermann in mixed open woodland consisting of *Ficus cotonifolia* and the endemic trees: *Bumelia socorrensis, Ilex socorroensis, Guettarda insularis,* and *Psidium socorrensis.* The family consisted of two adults and two immatures; the latter were fully grown and identical to the adults in appearance, except for yellow at the rictus. They still begged for food and were seen to be fed both insects and the olive-like fruit of *Bumelia* by their parents, although they were capable of foraging by themselves (fresh green shoots and dead crabs). The male sang and called loudly and appeared to be territorial, since he chased away a Northern mockingbird on two occasions. The female was more subdued and occasionally

"dueted" with her mate. In the same area we observed two individuals of the endemic Socorro lizard (*Urosaurus auriculatus*), a species that has probably also decreased due to cat predation.

Since the nidification of *Mimodes* is unknown, we searched in vain for a likely nest both in trees and on the ground. The only nest anywhere in the area was an old one, a large open cup on a tree fork, at a height of 3 m from the ground, probably of the Northern Mockingbird. All four birds were photographed (Vireo 527/7), videotaped, and recorded. Two other *Mimodes* were also seen and heard singing in the vicinity. The woodland where all six were found showed absolutely no sign of regeneration from the constant foraging by the abundant feral sheep. Later in the day below the crater of the volcano, we traversed a nearly intact forest with a lush understory showing no evidence of damage by sheep. Unfortunately we neither heard nor saw any *Mimodes* here, perhaps due to the lateness of the day. *Mimodes* was very tame and curious and readily came to inspect our photographic equipment and backpacks lying on the ground. Most of the time, however, it was arboreal and thus appeared less terrestrial than previously described (McLellan 1926). Perhaps those birds that have eluded the feral cats have done so by adopting a more arboreal existence.

Socorro Tropical Parula (*Parula pitiayumi graysoni*).—This endemic subspecies was the commonest land bird on Socorro in both open and wooded areas at all elevations. It was very tame, confiding, and inquisitive.

Socorro Rufous-sided Towhee (*Pipilo erythrophthalmus socorroensis*).—We found this endemic subspecies to be common in brushy and lightly wooded areas of Socorro. It was very tame and inquisitive, coming to inspect our feet and shoes as we hiked through brush. This behavior matches that described by Anthony (1898) but is in marked contrast to the shyness described by Jehl and Parkes (1982).

We did not find any American Kestrels (*Falco sparverius*), a species which has been considered a possible colonizer of Socorro (Parkes 1990) and has also been recorded from Clarión (Everett 1988). We also failed to find the Socorro Yellow-crowned Night-Heron (*Nyctanassa violacea gravirostris*) and the Socorro Elf Owl (*Micrathene whitneyi grayoni*), both endemic subspecies. Although feral sheep are causing serious ecological problems on Socorro such as erosion and lack of woodland regeneration, they do not appear so far to have affected the tree-nesting resident avifauna in the way feral cats have devastated the ground-nesting and ground-foraging birds (Socorro Dove, Socorro Mockingbird, and Townsend's Shearwater). On Clarión, although pigs have nearly destroyed all the prickly pear cactus (*Opuntia* sp.), the loss of this plant does not appear to have affected the resident land birds, since they were found in higher numbers than when Everett (1988) visited, at which time there were still extensive stands of *Opuntia*. The pigs, however, appear to have severely disrupted the breeding of Townsend's Shearwater and could adversely affect the breeding of the Red-footed Booby if they continue to destroy their nesting trees.

Clearly, control of the introduced animals is the number one conservation priority for the Revillagigedo Islands, since there are no apparent human pressures. Fortunately, both the Mexican civil government and the Mexican navy are now committed to the conservation of the islands, and feral animal control will be carried out and coordinated by the Centro de Investigaciones Biológicas of La Paz.

Roca Partida and San Benedicto are secure, and barring a new volcanic eruption on the latter, the number of nesting seabirds (possibly including Townsend's Shearwater) should continue to increase. We found seabirds numerous throughout the islands and the number of nesting species and populations matched fairly closely those observed by Howell and Webb (1990).

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Effects of leafing and position on nest predation in a Mediterranean fragmented forest.—Since Ricklefs' review (1969), it has been accepted that nest predation is a primary source of nesting mortality during the breeding season and is an important selective agent in the reproductive strategies of birds (Slagsvold 1982, Nilsson 1986). Hence, the choice of nest location could be a means of minimizing the effects of nest predation (Best and Stauffer 1980, Murphy 1983, Leonard and Picman 1987, Martin 1988a). Experiments using artificial nests have disclosed several factors affecting nest predation rates. In open nests and forest habitats, two of the main factors are vegetation cover and nest height. The former acts on the nest site and/or the nesting patch (e.g., Murphy 1983, Salathé 1987, Martin 1988a, Martin and Roper 1988) and may cause differences in predation rates among habitats. Likewise, Slagsvold (1982) has shown that in habitats with deciduous vegetation in which leaf phenology produces temporal changes in cover, the probability of nest predation varies throughout the reproductive season. Hence, species which breed after leafing (e.g., tran-Saharian migrants) should be less affected by nest predation than resident birds. With respect to nest height, higher positions have generally been found to be advantageous at temperate latitudes (Ricklefs 1969, Martin 1988b), although this advantage may be influenced by the cover in different vegetation layers (Slagsvold 1982, Yahner and Cypher 1987, Yahner and Scott 1988).

The present study is an experimental analysis of nest predation in a Mediterranean forest comprised of evergreen Holm oaks (*Quercus rotundifolia*), and deciduous Lusitanian oaks (*Q. faginea*). We hypothesized that the highest predation rates should be supported by nests with low cover, namely in Lusitanian oaks in early spring. Hence, nest predation should decrease in these trees after leafing, while it should be constant throughout the breeding season in the evergreen oaks. Holm oaks are thus controls which indicate variations in the predation pressure from causes other than cover such as variations of predator abundance or activity during spring (Slagsvold 1982, Smith and Andersen 1982, Yahner and Wright 1985). In this context, we also approached the influence of nest height on predation rates. We carried out our study in a fragmented forest. Recently, several authors have indicated that habitat fragmentation increases nest predation due to changes in the numbers and types of predators (e.g., Wilcove 1985, Martin 1987, Temple and Cary 1988). Cover and height advantages could thus be affected by fragmentation in our area, resulting in nesting patterns different from those evolved in more extensive habitats (Martin 1987).

Study area and methods.—The study area covers 525 ha in Villamayor de los Montes, Burgos province, in central Spain. The farming usage (dryland grain cropping and sheep grazing) has reduced the forest vegetation to a fragmented group of patches ranging from 0.1 to 90 ha, many of which are interconnected by small corridors. The arboreal vegetation has a mean height of 5.5 m and 35% coverage (22% Holm oaks and 12% Lusitanian oaks). The shrub layer (33% coverage and 0.7 m of mean height) is dominated by *Cistus* spp. The mean percentage of grassland is around 15%. Holm oaks and shrubby species are typical Mediterranean, evergreen plants, so their foliage cover is constant throughout the year, while the leaf phenology of Lusitanian oak causes the single cover differences among periods and sites in the study area. Hence, the foliage changes presumably do not affect ground cover, restricting to arboreal cover before and after Lusitanian oak leafing. Direct and indirect observations (footprints and feces), as well as trappings (Tellería et al. 1991), have shown that the area has a rich community of potential nest predators including corvids (Carrion Crow [*Corvus corone*], Black-billed Magpie [*Pica pica*], and Eurasian Jay [*Garrulus glandarius*], large and medium-sized mammals (wild boar [*Sus scrofa*], red fox [*Vulpes vulpes*], badger [*Meles meles*], weasel [*Mustela nivalis*], European Polecat [*M. putorius*] and western

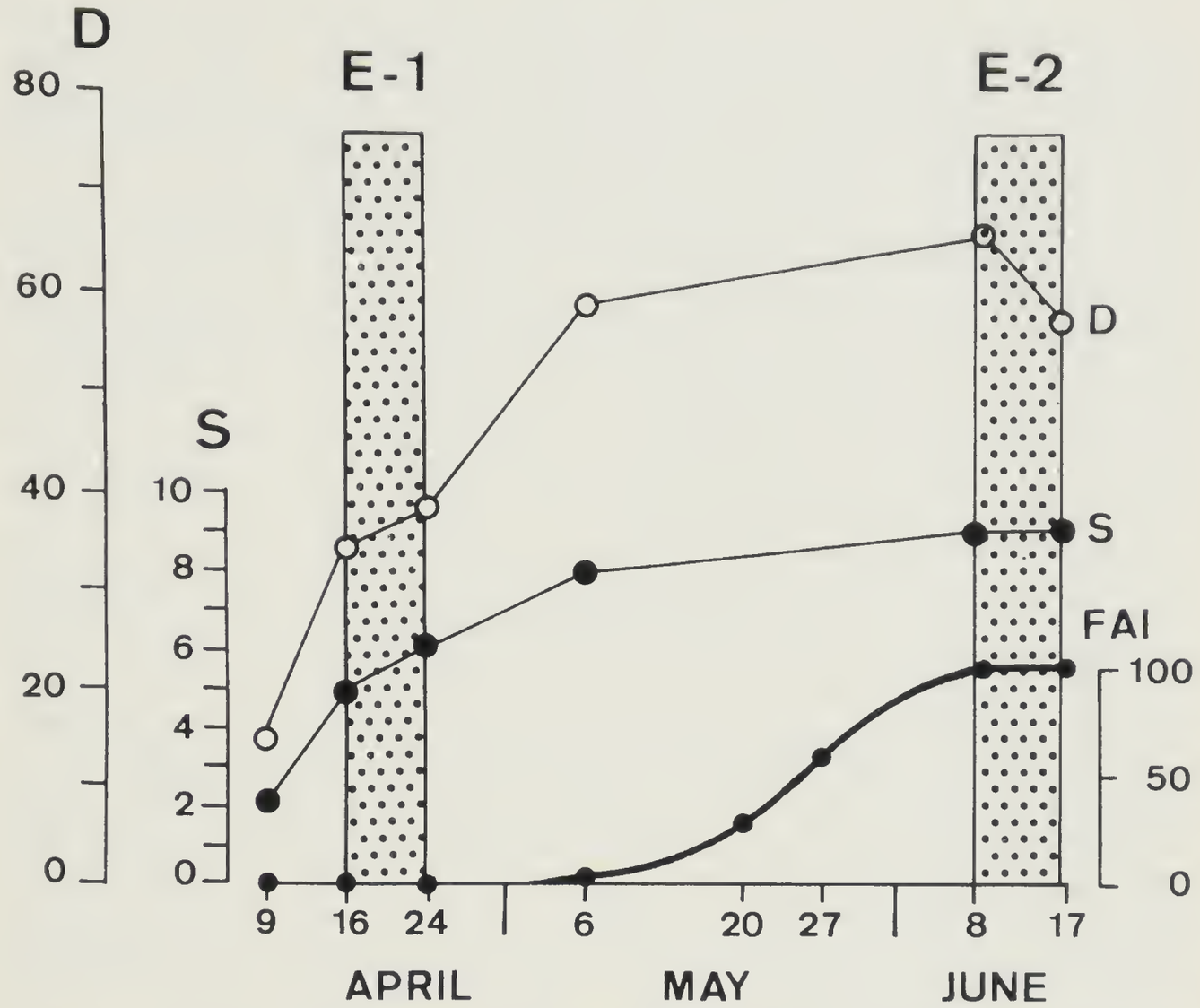

FIG. 1. Phenology of *Q. faginea* and summer passerines in the study area. D: density of summer passerines/density of passerines × 100. S: number of summer passerines. FAI: foliage area index, in percentages. E-1 and E-2 indicate dates of the first and second experiment, respectively. Migrant passerines: Subalpine, Orphean, and Bonelli's warblers (*Sylvia cantillans, S. hortensis,* and *Phylloscopus bonelli*), Common Nightingale (*Luscinia megarhynchos*), Brown Tree-Pipit (*Anthus trivialis*), and Ortolan Bunting (*Emberiza hortulana*). Resident passerines: Wood Lark (*Lullula arborea*), Common blackbird (*Turdus merula*), Robin (*Erithacus rubecula*), Great and European Blue tits (*Parus major* and *P. caeruleus*), Common Chaffinch (*Fringilla coelebs*), Common Serin (*Serinus serinus*) and Cirl Bunting (*E. cirlus*).

hedgehog [*Erinaceus europaeus*]), rodents (wood mouse [*Apodemus sylvaticus*] and garden dormouse [*Eliomys quercinus*]) and reptiles (ocellated lizard [*Lacerta lepida*]).

Lusitanian oak leafing phenology was monitored on eight occasions during spring 1988 (see Fig. 1 for dates), during each of which 2000 buds were sampled at random. The buds opened in May, after which time the number of leaves were counted, their length and width estimated, and an index of foliage area calculated by fitting the leaf form to an ellipse. Leaf cover was estimated for every date as the product of mean leaf surface by the number of leaves and further calculated as the percentage of the maximum value of full leafing (value 100%). Leaf growth accelerated in late May and was completed in early June when the Lusitanian oaks reached their maximum coverage (Fig. 1).

The arrival and settling of the migrant bird species was monitored along a 3.9-km transect

six times during spring, using the line-transect method (Järvinen and Väisänen 1975). The study area has nine migrant species, six of which are passerines (Fig. 1). At the start of April only Subalpine Warbler (*Sylvia cantillans*) was present, but by 6 May all species had arrived and maximum densities were reached. These species made up approximately 60% of the passerine community during May and the first half of June (Fig. 1).

Two experiments, each lasting eight days, were carried out. The first began before the sprouting of the first Lusitanian oak leaves and coincided with the arrival of the earliest migrant bird species. The second experiment took place after the completion of leafing and the arrival of all migrant breeders. Artificial nests were used, with a diameter of 9–10 cm and a depth of 5 cm. Two Japanese Quail (*Coturnix japonica*) eggs were placed in each nest. The nests were muddied for camouflage (Martin 1987) and placed in two positions: on the ground at the base of tree trunks and above ground level in tree branches. In each experiment 80 nests were arranged in each tree species, 20 on the ground and 60 on the branches.

The nests were placed alternately in Holm oak and Lusitanian oak, at a distance of approximately 30 m from each other, to avoid the formation of food patches which might influence the searching activities of predators (Martin 1988b). The nests were visited eight days after their placement, with no intermediate interference in order to avoid any influence on predation rates by our activities (Best and Stauffer 1980, Salathé 1987). The nests were re-located by means of natural features for the same reasons (Göranson and Loman 1986). Each nest where one or two eggs had been broken or were missing was considered depredated. We identified the nest predators by means of their feces, footprints and toothmarks (Bang and Dahlström 1972, Green et al. 1987). Feces and toothmarks indicated predation by rodents. Depredated nests with a lack of marks (apart from the loss of eggs) or which had been moved but without identifiable marks were assigned to unidentified predators (reptiles, birds and great mammals; see Best and Stauffer 1980, Green et al. 1987). Because of the scarceness of reptiles, we assumed that in this predator group the nests with a lack of marks were predated by birds, especially the Carrion Crow (see Loman and Göranson 1978, Fjeld and Sonerud 1988), the most abundant bird predator in the study area.

Results and discussion.—Predation on Holm oaks was similar in both experiments, thus confirming the similar predation pressure throughout the study period (Table 1). The number of depredated nests in both tree species was similar in the first experiment (Table 1) in spite of the lack of leaf coverage for nests in Lusitanian oak (Fig. 1). Likewise, the Lusitanian oak nests were subjected to the same predation in both experiments, before and after the leafing. There was no difference between experiments when the data from both tree species were pooled (Table 1). Both trees also supported identical predation in the second experiment (Table 1), showing a lack of further differences with both species in full leaf (χ^2, $P > 0.1$ in all the tests).

The distribution of nest predation in the two positions (ground and tree; Table 1) showed higher depredation rates on the trees in the two experiments separately ($\chi^2 = 12.987$, $P < 0.001$ for the first experiment; $\chi^2 = 3.708$, $P = 0.0542$ for the second experiment) and pooled ($\chi^2 = 17.455$, $P < 0.001$)

Depredated nests showed one or more of the following signs: garden dormouse (28) and wood mouse (4) feces; rodent toothmarks (44); and moved nests (129). These traces indicated that rodents, mainly garden dormice, were responsible for most of the mammalian predation. Rodent predation (feces and/or toothmarks) as opposed to unidentified predators (depredated nests without signs of rodents) is shown in Table 2. The activity of each predator group was the same in both experiments (χ^2, $P > 0.2$ in the two tests). The distribution of depredated nests between the two groups did not differ between experiments (χ^2, $P > 0.3$). Hence, the predator community had a constant action throughout the reproductive season, accounting for the lack of differences in predation rate between experiments.

TABLE 1

PERCENTAGES OF DEPREDATED NESTS ACCORDING TO TIME OF SEASON (SEE FIG. 1), TREE SPECIES, AND NEST HEIGHT (G: GROUND, T: TREE). THE NUMBER OF NESTS ARRANGED IN EACH TREE AND PERIOD WAS 80, 20 ON THE GROUND AND 60 IN TREES

Time of season	Tree species	Nest position		
		G	T	Totals
Before leafing	H Oak	65	90	83.75
	L Oak	60	88.3	81.25
	Totals	62.5	89.2	82.50
After leafing	H Oak	85	90	88.75
	L Oak	75	95	90
	Totals	80.0	92.5	89.38
Total	Both trees	71.25	90.8	85.90

The situation of depradated nests differed between both groups due to a greater rate of predation by rodents on the ground than in the trees compared with the unidentified predators ($\chi^2 = 6.5$, $P < 0.02$ for the first experiment and $\chi^2 = 9.9$, $P < 0.01$ for both experiments combined). Of the depredated nests attributed to birds, 16 were preyed upon on the ground and 92 in trees ($\chi^2 = 5.4$, $P < 0.02$ with respect to a random distribution in each situation).

These findings show that the increase in cover related to leaf phenology did not decrease the predation rates of the experimental nests, contradicting the importance it is generally given in temperate latitudes. The fragmented structure of the study area, however, could account for the high predation rate (e.g., Temple and Cary 1988, Møller 1989), which may decrease or nullify differences in predation due to leaf cover. Fragmentation leads to an increase in generalist predators (Janzen 1986, Temple and Cary 1988), forest remnants surrounded by agricultural matrices supporting high densities of corvids in temperate latitudes (Andrén et al. 1985, Angelstam 1986). In our area, crow abundance increases with

TABLE 2

PERCENTAGES OF NESTS DEPREDATED BY RODENTS AND OTHER PREDATORS ACCORDING TO TIME OF SEASON AND NEST HEIGHT (SEE TABLE 1). IN BRACKETS THE NUMBER OF NESTS PLACED IN EACH EXPERIMENT AND POSITION

Time of season	Height	Predator group	
		Rodents	Others
Before leafing	G (40)	27.5	35.0
	T (120)	15.8	73.3
	Totals	18.8	63.8
After leafing	G (40)	32.5	47.5
	T (120)	21.7	70.8
	Totals	24.4	65.0

fragmentation, very small fragments hosting the highest densities of crows. Differences in nest predation associated with cover could, therefore, emerge in larger fragments than those studied. In the conditions of our study, there is thus no apparent advantage in delaying breeding, at least with respect to the risk of nest predation. Likewise, resident birds do not gain any advantage from the greater Holm oak coverage in early spring. More work is necessary, however, to determine whether these results are typical of fragmented conditions. Similarly, studies designed on larger, less fragmented sites, are obviously needed to discriminate short-term effects caused by fragmentation from nesting patterns evolved through evolutionary time scales in extensive mixed forests (see Martin 1987).

The influence of nest position on the incidence of predators was, however, significant, in accordance with current ideas about its role in determining nest predation. In our study, predation was lower on the ground than at higher strata, perhaps indicating a lower incidence of mammals than in other studies where the opposite trend was found (see Ratti and Reese 1988, Yahner et al. 1989). The distribution of predation intensity between birds and mammals fitted, however, the general patterns found in other studies, where mammals mainly operated on the ground and birds were the primary predators on above-ground nests (e.g., Loman and Göranson 1978, Best and Stauffer 1980, Yahner and Cyper 1987, Møller 1988).

The observed differences in predation pressure between ground and tree nests could influence the organization of bird communities through the selection of nest position, according to Martins' ideas (Martin 1988b, c; see also Ricklefs 1989). If the fragmented structure of the studied forests was responsible for a part of the predation patterns found, however, we could expect changes in these patterns with respect to degree of fragmentation (Matthiae and Stearns 1981, Wilcove 1985, Martin 1987), via a variation in the predator community traits such as species composition and numbers and predator search tactics, which may be a source of local or more widespread variation (Slagsvold 1982, Martin 1987, Ratti and Reese 1988, Yahner et al. 1989). In this context, the dynamism of habitats and landscapes in temperate regions (Forman and Godron 1986, Yahner 1988) may induce a fast spatial and temporal turnover in predator communities and other factors affecting nest predation (e.g., habitat structure; see Wilcove et al. 1986).

As a consequence, we suggest that predation patterns and associated selective pressures are likely to be extremely dynamic and variable processes in many cases, operating on short time-scales (ecological time). Natural conditions, such as extensive and scarcely perturbed habitats, are hence required to investigate the importance of nest predation on evolutionary time.

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Pairbond formation in the Razorbill.—I report here the formation of a Razorbill (*Alca torda*) pairbond observed during a study of this species' mating system on Skomer Island, Wales, U.K., in the southern Irish Sea (51°40′N, 05°15′W) (Wagner 1991). Prior to egg laying, Razorbills that bred among boulders in the Basin study colony regularly attended two ledges near the entrance of the colony, which I refer to as "mating arenas." I observed color-banded individuals in the arenas on 44 mornings between 4 April and 24 May in 1988, for a total of 100 h in which birds were present, and for 52 mornings between 1 April and 26 May in 1989 for 125 h. In the same period, daily colony checks were made in which I recorded the attendance of individuals at numbered nest sites and their interactions with other Razorbills. I watched the arenas from a hide 25 m from the mating arenas with a 20–60 power spotting scope. Observations of the arenas began at first light, usually before any Razorbills had arrived from roosting at sea, and continued until most, or all, birds departed from the arenas or until their mating activities had virtually ceased.

Pairs performed 75% of their copulations in the arenas and the remainder in the nesting colony. Males frequently attempted extra-pair copulations, especially during the period in which females began to lay eggs, which began in the final week of April in 1988 and in the first week of May in 1989. For all copulation attempts I recorded the individuals involved, whether cloacal contact (and presumably insemination) was achieved, the number of cloacal contacts, and the duration of the mounting in seconds.

Almost all Razorbills that attended the arenas were paired, and mainly copulated with their mates, although 3% of successful copulations were with other individuals. Several unpaired males also attempted extra-pair copulations (EPCs) by copulating with paired

females, presumably to cuckold the pair male. However, unpaired males also attempted to copulate with unpaired females, apparently to acquire a mate. Here I describe the role played by copulation in Razorbill courtship leading to the formation of a pairbond between male "A," and female "B."

In April–May, 1988, A regularly attended the upper mating arena where he vigorously attempted to copulate with both paired and unpaired females. B had been banded as a nestling and was four years old when she was first sighted on 22 April. From then until 3 May, B visited both the upper and lower arenas on six days, departing and returning, making a total of 16 arrivals, and receiving six copulation attempts from males. One of these mountings was by an unmarked male who dismounted to fight with another male. After fighting, the unmarked male returned to B, who then accepted a copulation comprising one cloacal contact.

B's first encounter with A occurred upon B's arrival on the following morning. A mounted B, attempting to copulate, and B resisted aggressively but did not run or fly away, as was often the case when paired females resisted extra-pair copulations. However, two min later, B accepted a second attempt from A and fully cooperated in a 40 sec copulation which comprised three cloacal contacts; the male and female remained together following the copulation. During the next 28 min, B rejected three more copulation attempts by A, but they remained together after each one. During the three subsequent days, B made five arrivals but was not mounted by any other male except A, who attended during one of the three days. On 10 May, they performed one copulation of a single cloacal contact which was ended by the female. In the next 16 min, B refused three copulation attempts by A. In summary, B visited the arenas on 10 days and received 15 copulation attempts from at least three males, of which she accepted three and rejected twelve. Eight of the 15 mountings were performed by A.

It is probable that the first time I observed B and A together was their first encounter. I had observed the mating arenas every day from 4 April, and from then until B's first appearance on 22 April, A had attended on 11 days. If B was present together with A, I would almost certainly have identified her. It is informative to know that B's age was four years. Younger Razorbills arrive at the breeding areas later in the season and are not known to breed until the age of four, with five years being the modal age of first breeding (Lloyd and Perrins 1977).

I also spotted A and B at the breeding colony during nest checks. They were first seen at the colony on 5 May, two days after their first encounter in the mating arena. On 7 May, they prospected a potential breeding site together. On 12 May they performed a copulation of at least one cloacal contact which was ended by the female. They were together in the colony during all of the four days in which both were spotted between 5–13 May. B was not seen for the remainder of the season during subsequent colony checks, and may have returned to sea for the year, while A did attend the colony where he stood outside nests, attempting extra-pair copulations with the resident paired females. A continued attending the colony until the end of the breeding season, and was last seen 10 July, but did not acquire a mate.

In 1989, however, A and B attended the arena together as a pair. In a period of 20 days, A attempted 27 copulations of which B accepted nine. In that time, B received six EPC attempts and accepted none. The pair bred in a colony site near to where they prospected the previous year and produced an egg late in the season, which hatched.

This account reveals several features of Razorbill pairbond formation: (1) Copulations play a prominent role in courtship, (2) The mating arena serves as a meeting place for prospective mates, and (3) Pairbonds may be formed over a time scale which spans two years.

B's visits to the mating arenas were apparently aimed at acquiring a mate. Her behavior

suggests she made repeated visits to the mating arenas in order to receive copulation attempts from various males and that mountings may be a means by which females may appraise males. A was at least the third male sampled by B. Her rejection of A's first copulation attempt was aggressive. The fact that after her rejection of A, B did not depart, allowing him another attempt, suggests that B was there to appraise the male. B's resistance to most copulations provides evidence for the hypothesis that female birds may resist copulations as a ploy to appraise males (Westneat et al. 1990, Wagner, in press). Aggression over copulations in the mating arena is also compatible with the hypothesis that females incite male-male competition in order to appraise males (Cox and Le Boeuf 1977, Montgomerie and Thornhill 1989). It may be significant that B accepted a copulation from an unmarked male after he returned from fighting with another male.

Unpaired males may increase their fitness by cuckolding paired males (Trivers 1972). While B's aim in visiting the arena was apparently to find a mate, A performed a mixed strategy of courting the unpaired female, but also attempting EPCs with paired females. A male may not have been able to determine the mating status of a given female at first, but by his attempting a copulation, the female might have indicated her receptivity. Unlike B, who remained to be remounted after resisting B's first attempt, the reaction of most females was to flee after escaping from an EPC attempt.

Copulation may be used for courtship by many species (reviewed in Birkhead et al. 1987). Common Murres (*Uria aalge*) seem to form pairbonds in clubs (Birkhead 1985) where copulations also occur (Birkhead 1976). The Razorbill mating arenas differ from murre clubs in that the arenas are mostly attended by mature breeders, whereas clubs are attended by young non-breeders. The presence of paired female Razorbills in the arenas enabled unpaired males to pursue extra-pair copulations in the same location where they sought breeding partners.

Male Razorbills are not known to establish breeding sites to attract females. A did not defend a site, although he did visit unattended sites with B, after they apparently first met in the arena. However, three other unpaired males did defend a breeding site. All three had been paired and bred in their sites the previous year and were unpaired because their mates had not returned. While attending their territories, these males attempted to court unpaired females, suggesting that site ownership may be a means by which some male Razorbills obtain mates. In contrast to these three males, A was not seen to have bred in the previous year, suggesting that site ownership may be a mate acquisition tactic only used by experienced males who had owned the site previously.

A notable feature of pairbond formation in this account is the time frame. Although an association developed between the female and male in only several days, their courtship only led to a breeding attempt late in the following year. Prolonged courtship, presumably resulting in the careful selection of a mate, may be adaptive for long-lived species which retain the same mate for years. In this study, 35 of 39 (90%) of surviving pairs re-mated in the following year.

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Discovery of the Masked Saltator in Colombia, with notes on its ecology and behavior.— The Masked Saltator (*Saltator cinctus*) was described by Zimmer (1943), based on a specimen collected on the Cordillera de Cutucú, near Macas, Ecuador. Later, the species was collected in northern and central Peru, in the departments of Cajamarca, Amazonas, and Huánuco (O'Neill and Schulenberg 1979) and was observed again at the type locality (Robbins et al. 1987). Recently, it was observed by P. Greenfield et al. in Podocarpus National Park in southern Ecuador (Ridgely and Tudor 1989). It was seen in 1989 at two additional Ecuadorian localities, on the Cordillera de Huacamayos at ca 2000 m, south of Baeza along the road to Tena in western Napo and on the Cordillera de Sabanilla at 3000 m, south of Vilcabamba in Loja (Ridgely, in litt). The overall scarcity of observations suggests a patchy distribution from central Peru north to eastern Ecuador (Fig. 1).

I report here the discovery of the Masked Saltator in two Colombian localities (Fig. 1). Most observations have been made in the Reserva del Alto Quindío Acaime (4°37′N, 75°28′W), Municipality of Salento, Department of Quindío, on the western slope of the Cordillera Central. The first sightings took place on 3 and 4 December 1986. On 5 June 1989, I observed the species at the second site, located in the watershed of the Rio Blanco (5°04′N, 75°32′W) near the city of Manizales, Department of Caldas, 45 km north of the first site (Fig. 1).

Study area and methods.—The topography of the Alto Quindío is rugged and mountainous. The slopes between 2500 and 3650 m are covered with large remnants of primary forest interspersed with broad areas of secondary forest in different sucessional stages, tracts reforested with native species, and smaller areas of pastures and potato plantations. Above 3650 m, forest is replaced by páramo, and below 2500 m, the landscape is dominated by cattle pastures and small forest fragments. The forested area has been classified as "Lower Montane Moist Forest and Montane Wet Forest" (sensu Holdridge) (IGAC 1977). Rainfall

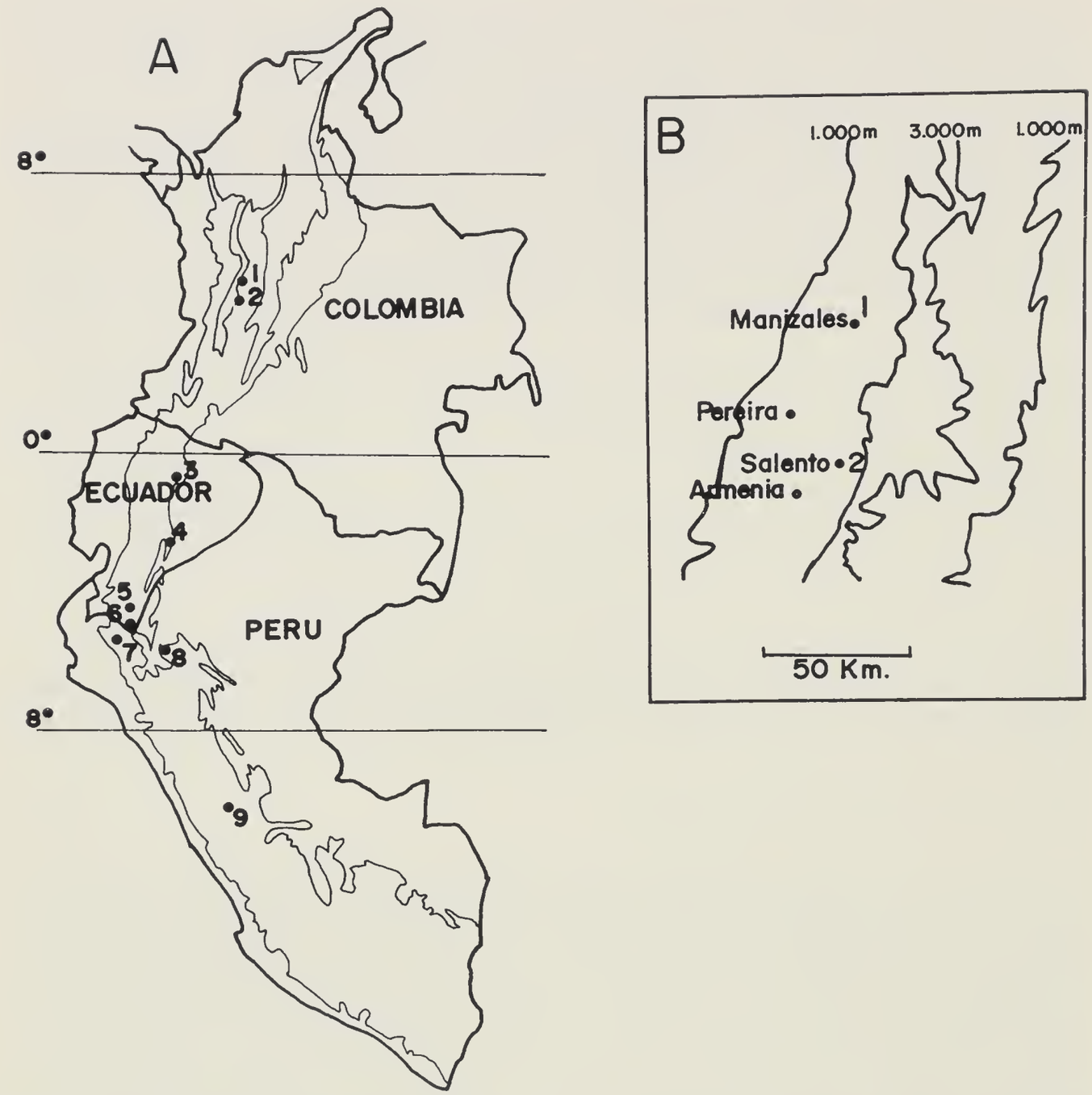

FIG. 1. A. Localities at which *Saltator cinctus* has been reported in the Colombian, Ecuadorian, and Peruvian Andes (the 1000 m contour is indicated): (1) Río Blanco, (2) Alto Quindío, (3) Cordillera de Huacamayos, (4) Cordillera de Cututucú, (5) Podocarpus N.P., (6) Cordillera de Sabanilla, (7) Cerro Chinguela, (8) Cordillera Colán, (9) Carpish. B. Central part of the Cordillera Central shown in detail.

is bimodal, with rainy seasons in April–May and October–November and dry periods in January–February and July–August (Pérez 1983).

From June 1989 through July 1990, I made four censuses each month, along each of four transects (total length 8.8 km) in the Alto Quindío. These transects included various types of primary and secondary forests, gaps, and the forest-páramo ecotone. To estimate the density of birds I divided the number of birds seen during all transects by twice the mean perpendicular distance from the transect for all individual sightings multiplied by the sum of the lengths of all transects (for further details, see Strahl and Silva, in press). An adult male was collected on 30 April 1991 and deposited in the bird collection of the Institute de Ciencias Naturales, Univ. Nacional.

TABLE 1
NUMBERS OF RECORDS OF THE MASKED SALTATOR IN DIFFERENT HABITATS AND STRATA IN ALTO QUINDÍO, COLOMBIA

Habitat	Strata			Total
	Understory	Middle	Canopy	
Primary forest				
Without *P. oleifolius*	0	0	6	6
With *P. oleifolius*	1	9	62	71
Edges and gaps				
Without *Chusquea*	6	1	1	8
With *Chusquea*	2	3	4	9
Secondary forest	5	0	8	13

Results.—The Masked Saltator is a distinctive bird (see Zimmer 1943, Ridgely and Tudor 1989). All the individuals seen in the Alto Quindío differ from descriptions in Zimmer (1943), O'Neill and Schulenberg (1979) and Ridgely and Tudor (1989) by having the bill wholly red, the belly creamy white instead of pure white like the chest, and a narrow pale gray streak behind the black mask. By these differences, the Colombian population may represent a different subspecies from those populations of Peru and Ecuador.

The Masked Saltator was observed a total of 108 times in the Salento area, between 2500 and 3080 m. It was found regularly in primary forest with *Podocarpus oleifolius* and *Prumnopytis montanus* (Podocarpaceae). These tree species are not uniformly distributed inside primary forest, but generally form patches on ridges and steep slopes. The birds were found year-round in the same places, suggesting that they maintain permanent territories. In the remaining habitats, I observed the species only sporadically (Table 1).

During the 1989–1990 censuses, I found an average of 17.2 individuals/10 km of trail in primary forest with *P. oleifolius* and of 1.2 individuals/10 km in the remaining habitats. The densities estimated were 82.6 birds/km and 5.9 birds/km in primary forest with *P. oleifolius* and in other habitats.

Since the forest with *P. oleifolius* comprises a very small proportion of total primary forest area (less than 10%), the Masked Saltator has a surprisingly low population density for a small frugivorous bird if this is compared with the densities reported for very large frugivores like cracids. Densities of 2.5–14.8 individuals/10 km of trail, and 1.8–19.8 individuals/km, were found for several cracid species in Venezuela (Strahl and Silva, in press) and Peru (Torres, in press).

The Masked Saltator is usually found in the canopy inside primary forest, and to a lesser extent in gaps and at lower heights along forest borders (Table 1). In Peru and Ecuador, *S. cinctus* was observed in thick stands of *Chusquea*, a common bamboo species of all localities where the bird was collected (O'Neill and Schulenberg 1979; Ridgely, in. litt.) and broadly distributed in the Andean cloud forest. I have also found Masked Saltators in *Chusquea* thickets, but those events appear to be occasional instead of reflecting an association with this bamboo *per se*. Indeed, the bird seemed, if anything, to avoid *Chusquea*, as it tended to descend to the understory along gaps and edges much more when bamboo was absent than when it was present (Table 1). Moreover, I never saw the birds foraging in the *Chusquea*, even when the stands were in seed. At Rio Blanco (the second locality), a pair was seen in

an area reforested with *Alnus acuminata* (Betulaceae), a native species which grows naturally in pure stands.

The Masked Saltator is inconspicuous, and few of my records were made before I learned its vocalization. The call can be described as a "tzip" (Vuilleumier 1970 and pers. obs.) or a "tseeyk" (Robbin et al. 1987), which is very similar to the foraging call of the Golden-fronted Redstart (*Myioborus ornatus*), but is more liquid (pers. obs.). This low-intensity call is repeated at irregular intervals when the bird is inactive or foraging, but as activity increases, the "tzip" is followed by a lower and softer "tiu-tiu." Robbins et al. (1987) found another vocalization that they described as a "chu" repeated at ca 3–5 sec intervals. I never heard this vocalization.

S. cinctus was usually observed singly (35% of sightings) or in pairs (61% of sightings). Only three times did I observe small groups, twice in December, 1986, and once in October 1989.

The Masked Saltator is an attendant species of mixed flocks (11% of sightings). The more frequent species in those flocks are Golden-fronted Redstart, Capped Conebill (*Conirostrum albifrons*), Pearled Treerunner (*Margarornis squamiger*), Spotted-crowned Woodcreeper (*Lepidocolaptes affinis*), White-throated Tyrannulet (*Mecocerculus leucophrys*), Sooty Brush-Finch (*Atlapetes schistaceus*), and Lacrimose Mountain-Tanager (*Anisognathus lacrymosus*). Vuilleumier (1970) once saw a Masked Saltator in a mixed flock.

Fruits and seeds are the most frequent items in the diet. I observed fruit consumption 36 times: 31 cases involved the fruit of *P. oleifolius,* two were arillate seeds of *Clusia multiflora,* two were unripe fruits of *Cissampelos* sp. (Menispermaceae), and one of an unidentified vine. I have also seen individuals foraging among fruiting *Siparuna echinata* shrubs, although I have not seen them consuming the arillate seeds. On one occasion a bird ate an unidentified young leaf.

Consumption of *P. oleifolius* fruits was seen essentially year round, both in wet and in dry seasons. This implies that the bird ate seeds at different stages of development. Moreover, the part of the fruit that normally attracts birds, the fleshy, red, sweet-tasting peduncle, was never consumed, but rather discarded, by *S. cinctus.* These observations, taken together, suggest that Masked Saltator is a predator, rather than a disperser, of seeds of *P. oleifolius.*

Breeding.—In the second half of April, 1991, I saw a pair of Masked Saltators very active and unusually low in a sector with very dense shrubs and *Chusquea* bamboo, near a stand of *P. oleifolius.* I assumed there was an active nest. On 29 April an adult flew out of these shrubs followed by a juvenile. The latter was duller than the adult, had a shorter tail, a small black mask and a pale yellow bill instead of red. It vocalized like an adult. Nearby, on a ridge with an open and stunted forest of *P. oleifolius* and *Clusia* sp., in a dense understory of Ericaceae, I saw another pair of Masked Saltators active at low levels. One of them was carrying nest materials. On 13 April 1990, I saw a saltator in an impenetrable tangle of ferns, possibly attending a nest. All those records have two elements in common: (1) the immediate proximity of *P. oleifolius,* and (2) saltators unusually active at low levels in very dense understory thus allowing the observer to approach them closely.

The male collected on 30 April 1991 was in breeding condition. One of the individuals observed at Rio Blanco on 5 June 1989 had a yellow bill (H. Alvarez, pers. comm.).

Discussion.—The records of *S. cinctus* presented here constitute a range extension of about 870 km northward. O'Neill and Schulenberg (1979) suggested that the species might occur in the southern Andes of Colombia. It is probable that the species occurs on the western slope of the Cordillera Central wherever there is adequate habitat. Its presence along the eastern slope of the Cordillera Central has yet to be confirmed.

The broad geographical distribution and few records of this very distinctive species suggest that it has a truly patchy distribution, probably due to specific habitat requirements. In the

Alto Quindío, at least, it shows a strong preferenee for highly loealized patehes of *Podocarpus oleifolius* within primary forest, where observation is difficult due to the steep topography. That may explain why the bird was missed by several very productive expeditions to the same area (Chapman 1917; Hernández et al. 1985; Orejuela, unpubl. data).

The Masked Saltator is a very vulnerable speeies beeause of its association with *P. oleifolius,* a tree speeies with a very slow growth rate that has been overcut beeause of its eoveted wood. The status of Masked Saltator in Colombia is of partieular eoneern sinee the Cordillera Central, the only range where the speeies has been found to date, is also the most deforested in the eountry (Orejuela 1985).

If the speeies is found in Eeuador in assoeiation with *P. oleifolius,* as is expeeted, its status there might also be precarious, as most of the Andean region is affeeted by colonization (L. Suarez, pers. eomm.). Additionally the prineipal forests of *Podocarpus* in Eeuador are found in Loja Provinee, the most deforested Andean area in the eountry, where the speeies is being strongly affeeted by timbering of the high quality wood, even within the borders of the Podoearpus National Park (L. Suarez, pers. eomm.) where the Masked Saltator has been recently seen (Ridgely and Tudor 1989).

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Fruit harvesting by American Robins: influence of fruit size.—Size relationships between bird gape width and fruit diameter can limit the composition and breadth of avian fruit diets and the disperser assemblages of plants with vertebrate-disseminated seeds (Wheelwright 1985, Snow and Snow 1988, Lambert 1989). It is less clear, however, that birds are influenced by differences in fruit size for fruits smaller than their gape capacities. Aviary studies with tropical species suggest that birds may prefer the largest fruits they can handle (Moermond and Denslow 1983); however, results from field studies have been mixed (Wheelwright 1985, Piper 1986).

Here we examine the hypothesis that the efficiency of fruit harvest by wild American Robins (*Turdus migratorius*) in New Jersey increases with increasing fruit size. A positive relationship between feeding efficiency and fruit size would suggest a possible rationale for size preferences in fruit-eating birds. American Robins, because of their abundance, diet, and relatively large size, are among the most important consumers of fleshy fruits in eastern North America (Wheelwright 1986, White 1989).

Methods.—We examined avian fruit foraging as part of a study of the nutritional content and value of fleshy fruits for birds (White 1989). Fruit consumption by American Robins was observed September–December, 1979–1982, in old fields and mixed-aged and mature woods in central New Jersey. We recorded the plant species visited, time from robin arrival to departure from the plant in seconds, and the number of fruits eaten. Fruit widths and masses for species used by the robins were determined from plants other than those used in the observations to avoid potential biases due to selective feeding. We recorded ten or more complete foraging bouts at each of the following plant species: *Rhus copallina, Juniperus virginiana, Rosa multiflora, Vitis vulpina, Viburnum prunifolium, Lindera benzoin, Nyssa sylvatica,* and *Pyrus* sp.

Results.—Mean fruit widths ranged between 3.7–9.0 mm in diameter (mean mass: 21–518 mg); however, size limitations in feeding were not at issue because all plants had fruits 3–8 mm narrower than the mean gape width of the robin (White 1989). Significant negative correlation existed (A) between fruit width and mean number of fruits eaten in a bout and (B) between fruit width and mean bout length, while significant positive correlation existed (C) between fruit width and total fruit mass harvested per bout (Fig. 1). Results were similar

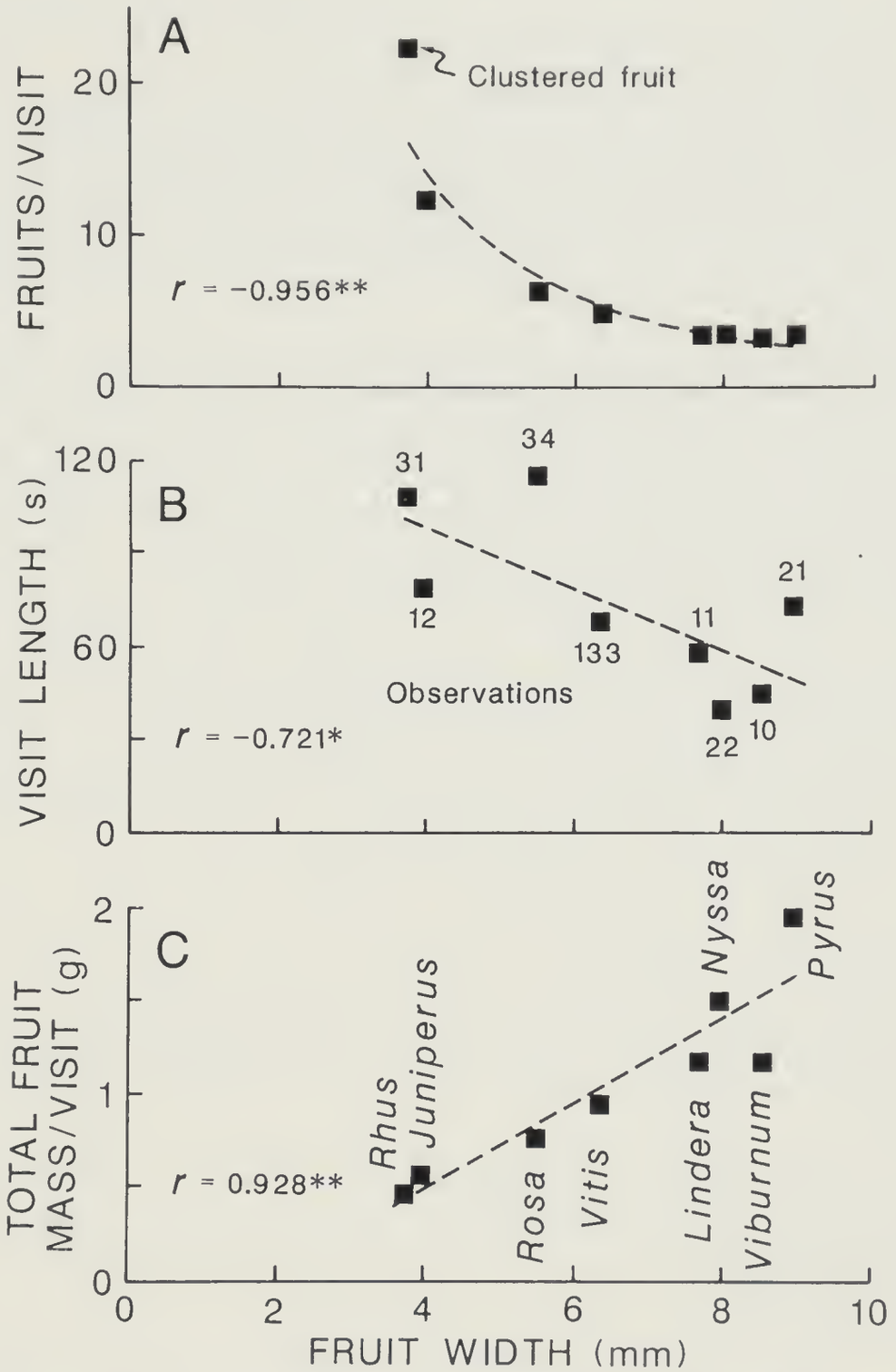

FIG. 1. Foraging by American Robins on fruits of eight woody species. A. Mean number of fruits eaten per foraging bout. Dense fruit clusters of *Rhus* sometimes allowed robins to feed easily from a single perch. The curve represents the power regression of fruits per visit on fruit width. B. Mean time spent in the fruiting plant per feeding visit. C. Total fruit mass consumed per visit calculated as the product of mean number of fruits eaten per bout and mean fruit mass. Numbers of complete foraging bouts observed are shown in Panel B.

when fruit mass instead of width was used as the independent variable ($r = -0.94$, $P < 0.01$; $r = -0.71$, $P < 0.05$; and $r = 0.98$, $P < 0.01$, respectively). Thus, robins fed on larger fruits more efficiently than smaller fruits, harvesting more biomass while swallowing fewer fruits in shorter visits.

Observation periods were not biased by fruit size. No significant correlation existed between fruit width and the time of day ($r = -0.08$, $P > 0.5$) or date ($r = -0.20$, $P > 0.5$) of observation.

From the birds' perspective, harvest efficiency may depend further on how much of the fruit is nutritive pulp and how much is non digested seeds. In the eight plant species examined here, 38–89% (mean = 31%) of wet fruit mass was pulp (White 1989). A positive relationship existed between percent pulp mass and fruit width ($r = 0.55$, $P > 0.1$); therefore, the total mass of pulp harvested per visit was also strongly positively correlated with fruit width ($r = 0.87$, $P < 0.01$).

Discussion.—Fundamental aspects of fruit harvesting by American Robins, including the number of fruits taken per visit, the length of a feeding visit to a fruiting plant, and the amount of whole fruit or pulp mass consumed per visit, were strongly associated with simple differences in fruit size. The results suggest that robins may have reason to prefer and select fruits approaching their gape capacities (cf Moermond and Denslow 1983). If size-related trends in harvest efficiency and fruit preference existed generally, the evolution of larger fruits might be favored even if enlarged fruits were available to fewer bird species because of limitations of gape size (cf Wheelwright 1985). However, the quality of seed dispersal might also vary with fruit size. If birds visit a small-fruited plant more often than a large-fruited plant to harvest an equal mass of pulp, then the spatial distribution of seeds could be more varied for the more-visited, small-fruited plant.

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Conspecific aggression in a Wood Stork colony in Georgia.—The probability of interactions among conspecifics, including aggression, is increased in colonial nesting birds. Increased egg and nestling loss due to the presence or activities of conspecifics represents a potentially severe cost of coloniality in many species of birds (Wittenberger and Hunt 1985). Nest losses to late nesters can result if nest material or suitable nest sites are in short supply. Nest or territory takeovers can also result if birds attempt to return to previous breeding sites that are already occupied, if there is a lack of unoccupied suitable nesting habitat, or if the net value of the breeding site exceeds the cost of the takeover (Johnson and Kermott 1990). There have been few studies concerning conspecific aggression among colonially nesting Wood Storks (*Mycteria americana*) or their allies. Barthos (1908) observed a pair of intruding White Storks (*Ciconia ciconia*) dislodge the resident pair of storks from a nest, throw out the eggs, and use the nest structure themselves. Kahl (1964) reported that nest attendance by adult Wood Storks during the early nestling stage is necessary to protect the young from inclement weather and "marauding bands of un-mated storks, which will attack and destroy unguarded nests." Frederick (1986) also observed nest takeovers and egg destruction among White Ibises (*Eudocimus albus*).

In this paper, we report on observations of nest takeovers, group aggression, and adults killing nestlings in a colony of Wood Storks in east-central Georgia. We describe this aggression, examine the variation in frequency of aggression among years, and discuss the possible consequences of these incidents and reasons for their occurrence.

Methods.—The Birdsville colony is located in Jenkins County, east-central Georgia (32°52′N, 82°03′W), on the northern edge of the Wood Stork's range. From 1986–1989 the colony included between 100 and 200 pairs of Wood Storks and 30 to 80 pairs of Great Egrets (*Casmerodius albus*). They nested in the tops of Cypress trees (*Taxodium ascendens*) in densities of one to 20 nests per tree. Storks began arriving at the colony in March and began nesting in late March and April (Coulter 1990). Hatching occurred from April through mid-June, and birds began dispersing from the colony in June through August, with some interyear variation. The period of time for storks to lay and hatch eggs and raise young to fledging age is about four months.

Nesting pairs of Wood Storks were observed from an 18-m tower within the colony for 7–12 h/day, five days a week, throughout each breeding season from 1986 through 1989. Pairs were considered established when eggs were seen in their nests or when adult behavior and posture suggested they were incubating eggs. We monitored 31–68 nesting pairs in the colony each year, including 10–20 pairs in which the sexes had been determined during copulation. Individuals were identified by unique facial and bill characteristics. Pairs were observed until their nestlings began leaving the nests or until the nests failed. Occurrences of conspecific nest takeover, group aggression, and nestling killing were recorded. Rates of agonistic behavior (incidents per hour) also were calculated.

Results.—Most nest takeovers followed the same progression of events. Two or more intruding Wood Storks would attack the adult stork or storks attending eggs or young nestlings. Attending adults were usually bitten on the head and neck for several minutes by the intruders before being forced off the nest. The eggs or nestlings were thrown from the nest in each case, and the new pair copulated on the nest within 10–15 min. Courtship behavior by the new pairs was rare.

Nest takeovers were observed primarily in 1988 (n = 12) and 1989 (n = 10), a single takeover was observed in 1987, and none was witnessed in 1986. In all instances, two or more Wood Storks attacked the resident adult(s). A single bird was never observed trying to force another stork from its nest.

Table 1

Average Number of Trips to Gather Nest Material by Pairs of Wood Storks at Takeover and Non-takeover Nests in 1988 and 1989

	Average number of nest material trips per hour			
	1988[b]		1989[b]	
Nest type[a]	N[c]	$\bar{x} \pm$ SD	N[c]	$\bar{x} \pm$ SD
Takeover	5 (121)	0.21 ± 0.23	5 (185)	0.17 ± 0.23
Non-takeover	8 (381)	0.32 ± 0.36	6 (300)	0.27 ± 0.37

[a] Takeover nests were acquired by conspecific aggression whereas non-takeover nests were initiated and maintained by the original pairs.

[b] Average nest material trips were significantly different between takeover and non-takeover pairs in 1988 (Wilcoxon Sum Rank test, $P < 0.01$) and in 1989 (Wilcoxon Sum Rank test, $P < 0.02$).

[c] N = Number of nests (number of nest-days of observation).

Eight nest takeovers occurred in which the sexes of the resident nesting individuals had been determined. In each of these cases, takeover attempts occurred when a single adult Wood Stork was in attendance. Seven of the eight attending adults at the time of the takeover were females. Resident pairs forced from their nests always attempted to drive the intruders away once their absent mates had returned. Only one pair regained its nest, but its young (1 nestling and 2 eggs) had already been thrown from the nest. This pair abandoned the nest site the following day. Two of the resident pairs that lost their nests were brooding at least one 1-week-old nestling, whereas the remaining six resident pairs were incubating eggs.

Nest takeovers should enable a pair of Wood Storks to spend less time and energy bringing material to the nest than would be required if they had initiated a nest themselves. To address this hypothesis, we compared the frequency of nest material trips made by intruding (takeover) pairs and resident (non-takeover) pairs in 1988 and 1989. Nest material trips per hour for all pairs varied significantly between years (Wilcoxon Rank Sum test, $P < 0.01$), and the data from the two years were analyzed separately. In both years, takeover pairs made significantly fewer trips than did resident pairs (Wilcoxon Rank Sum tests, $P < 0.02$; Table 1).

Only one of eight intruding (takeover) pairs successfully fledged young (3 fledglings). Six of the remaining seven intruding pairs produced eggs, and four of these pairs hatched young. However, all six breeding attempts failed either as a result of raccoon (*Procyon lotor*) predation or nest abandonment by the parents. The other attempt by an intruding pair resulted in one egg and was itself a victim of a nest takeover.

Group aggression involved more than four intruding Wood Storks fighting with one or more pairs of resident storks in nest trees and were frequently associated with nest takeovers. Group aggression began in at least two ways. First, intruding storks sometimes assembled in a tree containing nesting birds. Eventually, a resident stork or storks attempted to chase away an intruder and a fight ensued. The remaining intruding storks either participated in the fight or hovered near the nest tree.

Second, some group aggression followed other disputes, such as the theft of nest material. Within such disputes, resident Wood Storks responded to a threat with "bill-clattering" behavior (Kahl 1972). The snapping noise associated with this behavior seemed to attract storks from throughout the colony, resulting in group aggression.

We observed as many as 35 Wood Storks involved in a single group aggression. In that instance, three nests were taken over, and three new nests were later initiated by nonresident

TABLE 2

COMPARISON OF CONSPECIFIC AGGRESSION OBSERVED AMONG WOOD STORKS IN THE BIRDSVILLE COLONY, 1986 THROUGH 1989

Year	Hours (days) of observation[a]	Aggressive interactions observed[b]	Aggressive interactions/hour[c]	No. days aggression observed
1986	420 (40)	0	0.000	0
1987	433 (40)	3	0.008	3
1988	442 (43)	11	0.057	11
1989	520 (47)	45	0.086	20

[a] Observations in March, April, and May.
[b] Varied significantly among years (Kruskal-Wallis, $P < 0.01$)
[c] Varied significantly among years (Chi-square = 29.7, df = 7, $P < 0.01$).

birds that participated in the group aggression. We never observed lone parents abandoning their eggs or nestlings to join group aggression, but we observed adults that were attending incubating or brooding mates leave their mate to join the intruders.

Adult Wood Storks were observed throwing nestlings from neighboring nests on two occasions. In both cases, male storks were attempting to steal nest material from nests with young that were unattended by adults. On 28 May 1987, three nestlings were thrown from a nest within a 15-min period by a single neighboring male. An attack on 2 June 1987 resulted in the death of a single nestling from a brood of two nestlings.

Nest takeovers and group aggression were rare among Wood Storks in 1986 and 1987, but significantly more frequent in 1988 and 1989 (Kruskal-Wallis, $P < 0.01$; Table 2). Nest takeovers were also more frequent in 1988 and 1989, when they affected 13% (4/31) and 26% (18/69) of the observed nests, respectively, compared with 1986 and 1987, when they affected 0% (0/39) and 2% (1/51) of the nests, respectively. Numbers of days in which conspecific aggression was observed also were not evenly distributed among years (Chi-square = 29.7, df = 7, $P < 0.01$; Table 2).

Discussion.—Courtship behavior by storks is very important in the establishment of the pairbond and often occurs over a span of several hours to several days (Kahl 1971, 1972). However, there was a noticeable lack of courtship behavior in Wood Storks successful in takeover attempts, as well as in those storks initiating nests after incidents of group aggression. These intruding storks may have been paired prior to these nest takeover attempts. Ecological conditions conducive to early nest abandonment could result in paired storks that may attempt to acquire nests through agonistic behavior, an advantage of which is gaining an already built nest.

Early nest abandonments by Wood Storks were clearly linked to agonistic behavior with conspecifics. Abandonment of nests typically occurred only in the last half of the breeding season (June–August) in all years except 1989. These late-season abandonments were generally associated with increased predation as a result of drying conditions under the nest trees. In 1989, nests were abandoned as early as mid-April. Agonistic behavior in the colony peaked the week following these initial abandonments and continued into early May. Early abandonments in 1989 coincided with the week-long passage of a cold front in which temperatures dropped to 1°C and 9 cm of rain fell (Coulter 1990). The time budgets of nesting storks during this period indicated that they made fewer trips from the nest, stayed away for significantly longer periods on each trip when they did leave, and stayed at the

Table 3

Comparison of Average Duration of Trips from and Stays at the Nest, and the Number of Activities of Nesting Pairs in the Birdsville Colony, 1986 through 1989[a]

Year	Duration of trips from the nest (min)[bc]			Stay at the nest (min)[bc]			Number of activities per day[de]		
	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD
1986	96	196.1	104.2	156	183.2	126.7	41	7.3	3.1
1987	52	79.9	42.9	202	149.9	107.7	35	7.8	4.0
1988	50	160.1	99.8	118	174.5	136.7	25	6.0	2.8
1989	25	297.8	115.2	68	333.8	152.1	37	3.4	5.6

[a] The time budgets analyzed here compare the trip length and number of activities of nesting pairs during the week-long passage of a cold front in 1989 to the time budgets of nesting pairs of a similar reproductive stage in the previous three years.

[b] Trips and stays at the nest less than 30 min in duration were not included in an effort to distinguish the longer foraging trips from the shorter trips to acquire nest material.

[c] Average duration of trips and stays at the nest were significantly different among years (Kruskal-Wallis tests, $P < 0.01$).

[d] Activities included any trip in which the bird returned to the nest.

[e] Average number of activities for nesting pairs in 1989 was significantly lower than that in 1986, 1987, or 1988 (Mann-Whitney U tests, $P < 0.01$). There were no other significant differences among years (Mann-Whitney U tests, $P > 0.05$).

nest for longer periods after returning (Kruskal-Wallis tests, $P < 0.01$; Table 3). Kahl (1964) suggested that cooler temperatures could hinder the storks energetically during the stressful courtship period and could negatively affect the availability of prey by making them less active and, presumably, more difficult to capture. Heavy rainfall can increase surface water levels at foraging sites and disperse prey. Thus, storks may have needed more time to locate and capture food during this period.

In 1988, another year with frequent nest takeovers and group aggression, abandonment of Wood Stork nests in the first half of the season was not noted. However, that year the storks arrived at the colony site about one week later than normal and in lower numbers than the previous two years (Coulter 1989). March and early April of 1988 was characterized by considerable movements of large groups of nest-building storks from one tree to another. These movements appeared to occur before any eggs were laid, but many birds may have been paired prior to abandonment. Storks may have arrived late in 1988 as a result of poor feeding conditions on their wintering grounds so that the birds may have needed more time to reach breeding condition. Also, the late arrival could have made the acquisition of an already built nest more advantageous.

Taking over an active stork nest can be beneficial to potential nesters if either nest material or suitable nesting sites are in short supply. Although not quantified in this study, nest material and suitable nest sites seemed abundant in the colony each year, and we could not discern a preference or advantage of a particular type of nest site. Also, neither nest density nor location in the colony affected the likelihood of predation when predators (raccoons) invaded the colony.

Wood Storks involved in nest takeovers were socially or behaviorally atypical. Mutual manipulation of nest material by nesting Wood Storks is a behavior that maintains the pairbond throughout the lengthy breeding season (Kahl 1972). Whereas the reduced number of nest material trips by takeover pairs was energetically beneficial, it also effectively reduced

the opportunity to reinforce the pairbonds of these birds and suggests a weakness in the pairs themselves.

Nest takeovers and group aggression at the Birdsville colony usually occurred from late March through May each year when most birds were building nests and laying eggs. Renesting by Wood Storks was occasionally successful. We observed a color-banded Wood Stork attempt to nest three times at different sites within the colony early in the same season and successfully raise young from the third attempt to fledging age. Most takeover pairs were not successful nesters. Nest takeovers seem to be attempts by paired birds from early abandonments to save time and energy by renesting as quickly as possible in already built nests. However, such attempts have a reduced likelihood of success because of increased risk of predation as a result of nesting later in the season and possible weaknesses in the pairbond of the takeover pairs.

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Foraging behavior of a guild of Neotropical vultures.—Coexistence of two ecologically similar species within a habitat is achieved by the evolution of some degree of difference in resource use. By feeding on different foods, at different sites, or with different foraging behaviors, species can avoid competitive exclusion. Avian scavengers, which feed upon an unpredictable and ephemeral resource, may finely divide their food resource along one or more resource axes in order to survive. Wallace and Temple (1987) demonstrated that scavengers presented with very large carcasses in open habitat showed interference competition by establishing a dominance hierarchy among species locating the resource. This guild of New World avian scavengers formed a dominance hierarchy with Andean Condors (*Vultur gryphus*) on top, followed by King Vultures (*Sarcoramphus papa*), Crested Caracaras (*Polyborus plancus*), Turkey Vultures (*Cathartes aura*), and Black Vultures (*Coragyps atratus*), in that order. These authors observed feeding at large carcasses in open areas that were frequented by all the species of scavengers in the guild. The largest carcasses were opened to make them available to small scavengers and larger scavengers at the same time. More than half of the carcasses provided were burros (*Equus asinus*). In the forested areas of the tropics, this type of resource is unavailable. Houston (1984a) showed that most of the biomass available to vultures on Barro Colorado Island, Panama, comes from animals with masses less than 3 kg. In addition, differences in foraging behavior and sensory physiology may make carrion in forest habitats less available to some species of scavengers than to others. Niche overlap may be quite different for avian scavengers feeding on small carcasses in a tropical forest than it is for those same scavengers feeding in a coastal desert. In a tropical rain forest, competition for a dispersed, ephemeral resource may depend upon differential exploitation rather than interference.

Here I describe the interactions among the species in a guild of Neotropical vultures in a complex, natural environment. The carcasses used were not large and they were presented to the vultures in a variety of habitats. This method was intended to approximate the distribution of carcasses that a vulture would normally encounter in the rain forest. It is my hypothesis that vultures feeding in the rain forest use differential exploitation to avoid competitive exclusion. In this paper, I will discuss niches separated in space and along a time axis. Cody (1974) stated that time is only important to competition and coexistence due to seasonal shifts in the species composition of communities. I will provide an example in which differences in resource use by Neotropical vultures at different times allow coexistence of closely related and ecologically similar species.

Study site and methods.—This study was conducted at Estacion Sirena in Parque Nacional Corcovado on the Osa Peninsula in southwestern Costa Rica (8°26′N, 83°35′W) from June to August 1987. Turkey Vultures, Black Vultures, King Vultures, and Lesser Yellow-headed Vultures (*Cathartes burrovianus*) are sympatric in the coastal regions of Corcovado (Stiles and Janzen 1983). Estacion Sirena is adjacent to the Pacific Ocean and is surrounded by a patchwork of primary tropical wet forest (Herwitz 1981, Hartshorn 1983), second growth forest of various ages, gaps in the forest, and beach. Historically, portions of the area have been the sites of intensive agricultural use, but since the establishment of the park in 1975, the vegetation has been allowed to recover. The primary forest is characterized by a continuous canopy more than 10 m from the ground and a sparse understory. Due to the historical land use of this area, most of the primary forest is located on rough terrain (hillsides, ridges, etc.), with the exception of one large patch of forest on flat terrain adjacent to the ocean. The second growth forest is characterized by dense stands of *Heliconia* spp. and *Calathea* spp. This dense growth is typically 2 to 5 m tall and fairly homogeneous. There are frequently tall, slender trees (i.e., *Cecropia* spp.) emerging from this dense growth, but

the canopy is far from complete. As a result, much sunlight reaches the understory which is nearly impenetrable. The gap habitat is an area of mown grass surrounding the station and on the airstrip southwest of the station. This area is constantly maintained and lacks all vegetation except for herbal growth less than 20 cm tall. For this study, the beach, which lacks all vegetation, and the airstrip will be called gap habitat.

Resource partitioning and habitat use were studied by observing the feeding locations and behavior of all four species of vulture at carrion placed at several locations in each of the three habitats. Carrion baits were 33 similarly sized (3–5 kg) fresh, whole fish carcasses (*Caranx* spp.). The carcass of a spinner dolphin (*Stenella longirostris*) which was found shortly after it had died was also included in the study. Carrion placed in primary forest was completely obscured from above by the forest canopy which was 20 to 50 m above the ground. Carrion placed in the secondary forest was completely obscured from above by the dense understory. Carrion in open habitat was not obscured at all. Carcasses were concealed until they were placed on the ground at mid-day when the vultures were typically roosting. No carcasses were placed near roosts and no vultures were in view when the carcasses were distributed.

Each carcass was observed each day until it was totally consumed. To avoid disturbing the birds, observers remained 50 m or more away from the carcasses and observed the vultures using 10× binoculars and a 25× spotting scope from a concealed position. Observers were located in positions that provided views of the carcass, surrounding ground and vegetation, and a large portion of the sky above the carcass. The time course of vulture arrival and carrion consumption was recorded in days from the time that the freshly caught fish was placed out for the vultures.

In this study the resources considered were habitat type (gap, secondary forest, and primary forest) and age of the carcass (days since first available). The data collected were not adequate to determine the number of individuals of each species feeding upon each carcass, but the species feeding upon each carcass were identified. Since individual birds arrived at carcasses at different times and left after short feeding bouts, birds would have had to have been individually marked in order to estimate numbers of each species present. The numbers in the data represent the occurrence of one or more individuals of that species feeding on a single carcass on that particular day. Each observation could represent one or more individuals of a single species.

Results.—The composition and behavior of feeding aggregations were different depending upon where the food was located. When carrion was placed in the open gap habitat, either Turkey Vultures or Black Vultures were the first species to arrive and feed. Feeding aggregations in the gap habitat could be very large with three or four species represented, but no interspecific aggression or even casual displacement was observed. Intraspecific aggression was common only among Black Vultures. In the secondary forest, perhaps due to limited visibility and open ground, Black Vultures and Turkey Vultures foraged and fed individually or in small single species and mixed species groups. No interspecific aggressive encounters or displacements were seen. Under the primary forest canopy, where carcasses were obscured from view of birds above the canopy, Turkey Vultures or King Vultures were the first species to arrive. King Vultures were frequently the first birds to locate a carcass and would feed upon it before Turkey Vultures arrived. On one occasion, Turkey Vultures located a carcass 15 m away from the edge of a gap in the primary rain forest. They approached the carcass from downwind, flying back and forth perpendicular to the wind direction. As they were approaching and descending toward the carcass, a large group of Black Vultures from a nearby roost tree joined them. The Turkey Vultures began feeding first, and the Black Vultures began feeding moments later.

Vultures fed upon 18 carcasses in three different habitats (Fig. 1). On many occasions, more than one species fed upon the same carcass, and in all cases more than one individual

bird fed on each carcass. Turkey Vulture feeding activity was widely distributed in all three habitat types. Black Vulture feeding activity was concentrated around the gap habitat and highly disturbed areas of the adjacent forests. In both cases where Black Vultures fed in the primary forest, they landed in the open habitat and walked under the canopy. Most of the carcasses fed upon by King Vultures were in the primary rain forest, except for the spinner dolphin on the beach. This was also the only site where Lesser Yellow-headed Vultures were seen feeding. All four species were seen feeding on the dolphin on the same day.

Most feeding occurred the day after the fresh carcasses were made available. Carcasses made available on Day 0 were seldom fed upon until Day 1. In subsequent days, the number of feeding vultures decreased steadily due to consumption of the carcass. Few carcasses were still present beyond Day 4, and any feeding that occurred during this time was included in Day 4. Black Vultures and Turkey Vultures were observed on every day while King Vultures were not seen feeding on very fresh carcasses or carcasses more than four days old.

The temporal distribution of feeding varied among the three habitats (Fig. 1). Every species fed in the open habitat, with Turkey Vultures present only on the first three days and Black Vultures present on all days. King Vultures fed only on Day 1 and Day 2. The temporal distribution of feeding in secondary forest was very different, with only two species represented. The temporal distribution of feeding in the primary forest indicates that no feeding occurred on Day 0 and that the feeding was dominated by two species, Turkey Vulture and King Vulture.

Discussion.—Vultures feed on an unpredictable and ephemeral resource. Most of their foraging energy is spent searching for carrion, and when they find carrion, they are observed by other vultures which quickly follow them to the food source. The carcasses they feed upon are usually not large enough to allow all vultures to feed without some intraspecific or interspecific competition. In addition, the carcasses decompose rapidly and are only available to the vultures during a brief time period. As a result, many vultures are forced to feed upon a limited resource at essentially the same time.

Cathartid vultures in the lowland tropical rain forest of Costa Rica partition their feeding behavior spatially and temporally. A similar guild structure has been seen in accipitrid vultures in East Africa (Kruuk 1967). There, as here, the character of the resource changed over time and species with the appropriate adaptations were able to use the various resource states as they occurred.

The method that vultures use to locate carrion also affects the temporal segregation of feeding. The species that feeds on a carcass first should be the species that detects it first. Turkey Vultures probably use olfactory cues to locate food while Black Vultures rely on vision (Stager 1964, Houston 1986, but see Smith and Paselk 1986). Stewart (1978) suggested that Black Vultures seem to follow Turkey Vultures to carrion. In this study, Black Vultures arrived first at carcasses in the open where they were highly visible, but arrived second at carcasses under the forest canopy where olfactory cues may have been more important. It appears that the species that was most proficient at detecting carrion in each habitat arrived first. The less proficient species had to rely on cues from the other species to provide information about the location of food. Carrion placed in the open gap habitat was located quickly because more species were proficient at detecting it. All cathartid vultures have acute eyesight and are able to find carcasses that are visible from above. Carcasses that were on the forest floor were harder to detect. Only those species that have the ability to detect carrion by using non-visual cues could locate it. As a result, feeding began later on carrion in primary and secondary rain forest than it did in the gap habitat.

Little is known about the foraging behavior or physiology of King Vultures and Lesser Yellow-headed Vultures. Houston (1984b) suggested that King Vultures were unable to detect carrion by the use of olfactory cues. In this study, King Vultures were able to locate

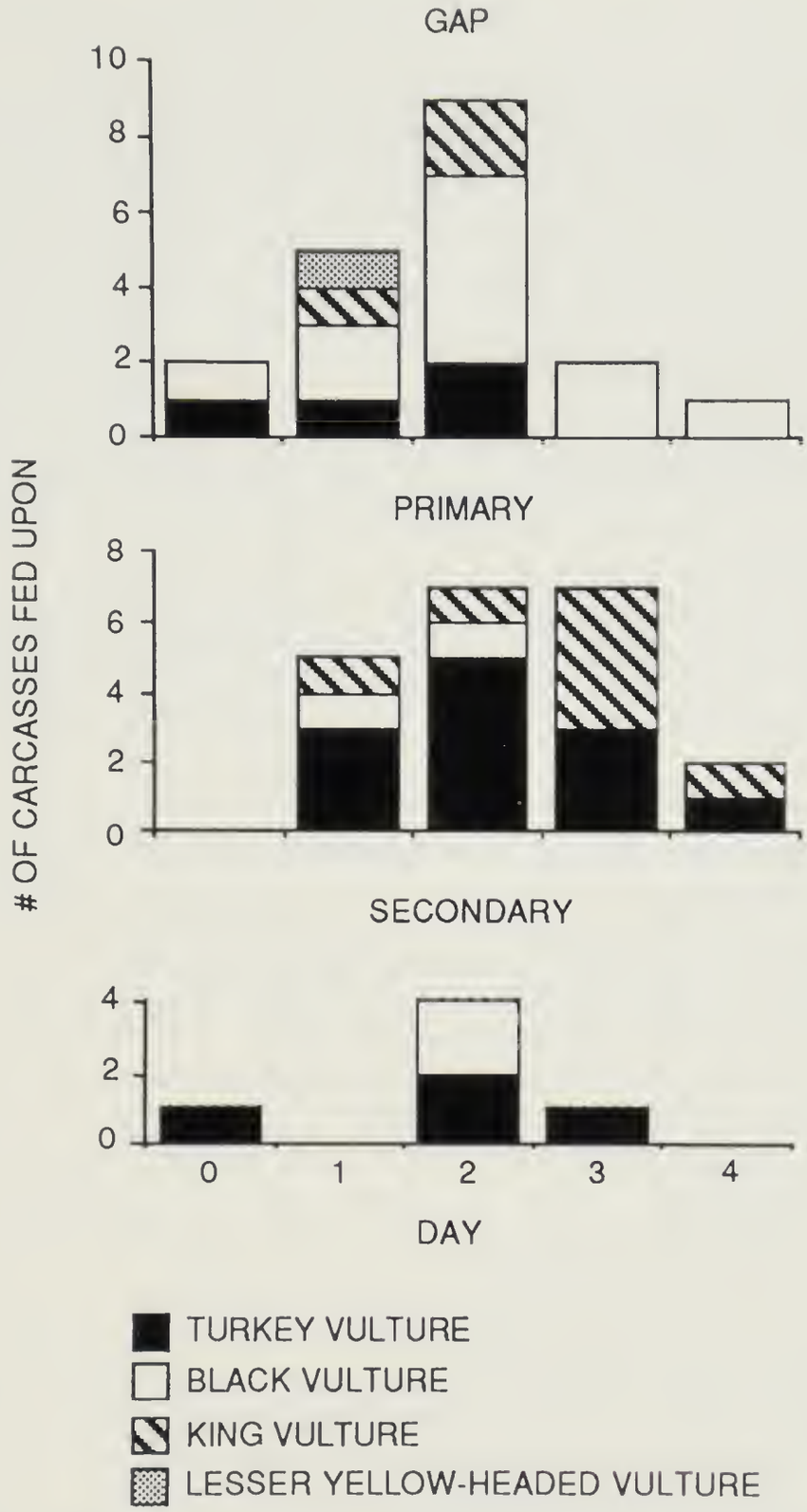

FIG. 1. The temporal distribution of vultures feeding in three habitats.

carrion beneath the closed primary forest canopy independent of Turkey Vultures. Although the physiological evidence that King Vultures use olfaction to locate food is not available, this study shows that King Vultures use cues other than visual cues, such as olfaction, to locate carrion in the forest. A more detailed study of the physiology and behavior of carrion detection by the King Vulture is needed.

In a relatively undisturbed tropical rain forest environment, cathartid vultures do not feed in the same habitats. Black Vultures specialize on carrion located in the open, while

King Vultures are forest specialists. Turkey Vultures are habitat generalists, feeding in the open and in the forest, but they separate their feeding from the other species temporally. Turkey Vultures specialize in carrion that is relatively fresh. In most cases, they locate it first and leave before individuals of other species arrive in great numbers. King Vultures feed on carrion that is slightly older, but they too leave while carrion is still available. Black Vultures are temporal generalists and will eat anything. They will commonly feed upon a carcass for two days after the last Turkey Vulture or King Vulture has departed.

The community structure of this guild of vultures closely parallels that of the accipitrid vultures in the open savannah of East Africa (Kruuk 1967). In that community the White-headed Vulture (*Trigonoceps occipitalis*) was typically first to arrive at a carcass and the White-backed Vulture (*Gyps africanus*) was a temporal generalist. Avian scavengers in the open agricultural land of Peru showed a similar temporal displacement pattern (Wallace and Temple 1987). The results reported here show that the temporal organization of a guild of avian scavengers was dependent upon the habitat in which they fed and upon the method used to detect carrion.

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Ovarian follicles do not reveal laying histories of post-incubation Wood Ducks.—Post-ovulatory follicles (POFs) are ovarian structures from which mature oocytes have ovulated. Although POFs have been used to determine the frequency of ovulation in many avian species (Table 1), little has been published on their use in anatids (Ankney 1974, Ankney and Afton 1988). This note reports the results of a pilot study to see if the POFs of female Wood Ducks (*Aix sponsa*) that were collected just after their young hatched could be used to determine the number of eggs each female ovulated and (presumably) laid in the immediately previous laying sequence.

We examined the ovaries of five captive two-year-old female Wood Ducks in 1989. Females and their mates were maintained from pre-laying until the completion of incubation in individual 1.1 × 3.1 m enclosures at the Max McGraw Wildlife Foundation (MMWF). Each pair was provided commercial laying pellets and water ad lib and a nest box. Clutch sizes ranged from 9 to 12 eggs ($\bar{x}$ = 10.2, SD = 1.1). Females were permitted to incubate full-term (ca 30 days) and were sacrificed one day after young left the nest box. This time of collection was selected to provide an easily implemented criterion for possible future collections of birds that had nested in natural cavities, i.e., females with recently hatched young would certainly have completed laying in the current reproductive bout, regardless of whether it was their first or second clutch.

Intact ovaries were removed immediately from sacrificed females and fixed in 10% neutral buffered formalin. Ovaries were examined under a dissecting microscope using Payne's (1966, 1973) descriptions of post-ovulatory and atretic (regressing unovulated) follicles as a guide. Independent inspections for POFs were made by both authors, an avian reproductive physiologist (A. van Tienhoven, Cornell Univ.), and a wildlife biologist (S. M. Byers, MMWF). The ovaries were coded upon removal, and none of these individuals knew the number of eggs laid by each female when he inspected the ovaries.

Results were disappointing: thorough examinations of fresh and preserved ovaries revealed no evidence of follicles. Pigmentation indicative of the terminal stages of involution also was absent. We did not section the ovaries because the effort and expense were not justifiable, given that no follicular remains were visible (R. B. Payne, A. van Tienhoven, pers. comm.). Sacrificing more birds simply to increase the sample size also did not seem justified.

In areas intensively managed for Wood Ducks in which groups of nest boxes have been erected in the open, the frequency of intraspecific brood parasitism ("dump nesting") is high relative to situations where the birds nest in dispersed, well-hidden boxes (Semel et al. 1988, 1990). As suggested by Semel et al. (1990), this difference in parasitism may result either because (1) individual females lay more eggs when boxes are clustered in the open, perhaps stimulated by frequent opportunities for parasitism, (2) females are attracted to active nest boxes and thus lay a greater proportion of their eggs parasitically, or (3) greater numbers of females congregate in areas with numerous, visible boxes. Accurate determinations of the number of eggs ovulated by individual females during any given reproductive bout are necessary to decide among these alternatives.

Testing hypotheses 1–3 (above) requires comparisons between females nesting in natural cavities and those nesting in clustered, visible boxes. However, natural cavities in which Wood Ducks nest are widely spaced and well hidden in most areas (e.g., Soulliere 1990), making collection of an adequate sample of incubating females from them prohibitively difficult. Therefore, we did not examine whether the POFs of Wood Ducks remain distinguishable during early incubation. Females in association with recently hatched ducklings (i.e., "Class Ia" young: Gollop and Marshall 1954) are more easily collected, and we had hoped to use their POFs to distinguish among our hypotheses. Unfortunately, however, our

TABLE 1

LENGTH OF TIME POST-OVULATORY FOLLICLES PERSIST AS DISTINGUISHABLE STRUCTURES IN VARIOUS BIRDS

Species	Time[a] (days) post-ovulatory follicles remain distinguishable	References
European Starling (*Sturnus vulgaris*)	≥7.5 s[b]	Kennedy et al. 1989
Black-billed Magpie (*Pica pica*)	<12 s	Erpino 1969
Jackdaw (*Corvus monedula*)	≥12 s	Hett 1923 (in Payne 1966)
Rock Dove (*Columba livia*)	<30 s	Davis 1942
Yellow-billed Cuckoo (*Coccyzus americanus*)	≤14 s	Payne 1973
Red-winged Blackbird (*Agelaius phoeniceus*)	≤25 s	Payne 1966
	≤12 m	
Tricolored Blackbird (*A. tricolor*)	≤25 s	Payne 1966
	≤12 m	
Brown-headed Cowbird (*Molothrus ater*)	≤25 s	Payne 1965
	≤12 m	
Fulmar (*Fulmaris glacialis*)	≥365 s	Wynne-Edwards 1939 (in Payne 1966)
Domestic Fowl (*Gallus gallus*)	≥28 s	Davis 1942
California Quail (*Callipepla californica*)	<10 m	Lewin 1963
Blue Grouse (*Dendragapus obscurus*)	≥149 m	Standing 1960
	≤33 m	Hannon 1981
Sage Grouse (*Centrocercus urophasianus*)	unreliable m	Dalke et al. 1963
Ring-necked Pheasant (*Phasianus colchicus*)	≥73 m	Buss et al. 1951
	≥15 m	Meyer et al. 1947
	≤100 m	Kabat et al. 1948
Snow Goose (*Chen caerulescens*)	≥24 m	Ankney 1974
Wood Duck (*Aix sponsa*)	<30 m	This study

[a] There is considerable variability in research design among studies. In this table (≥) means that POFs were still distinct for at least that number of days (and possibly longer), (≤) means that this was the maximum number of days POFs remained distinct, and (<) means that POFs regressed at some prior but unknown time.

[b] Laboratory techniques involving (m) macroscopic examination or (s) serial sectioning.

results indicate that Wood Duck ovarian follicles regress beyond recognition by the end of incubation. A different research approach (such as DNA "fingerprinting," Burke 1989) will be required to determine the mechanisms underlying super-normal brood parasitism in intensively managed Wood Duck populations.

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A note on the vocalizations of the Chinese Nuthatch.—Within the rather uniform genus *Sitta* there is a species group of four small conifer-dwelling nuthatches: Corsican Nuthatch (*Sitta whiteheadi*), Kabylie or Algerian Nuthatch (*S. ledanti*), Kruper's Nuthatch (*S. kruperi*) in Asia Minor, Chinese Nuthatch (*S. villosa*) in eastern Asia. These nuthatches have a highly disjunct distribution in the Palearctic region. Interest in this group has been stimulated by the recent discovery of *S. ledanti* (Vielliard 1976). Though some comparative information is available on the three Mediterranean species concerning voice, general behavior and details of plumage (Löhrl 1961, Ledant and Jacobs 1977, Ledant 1978, Vielliard 1978, van den Berg 1982), little is known about the Chinese Nuthatch (Löhrl 1988). This species is of particular interest as it is regarded as the most primitive member of the genus (Vielliard 1978). Here we describe vocalizations of the Chinese Nuthatch recorded in the province of Sichuan, China, and discuss the relationship with vocalizations of the Mediterranean nuthatch species.

Study area and methods.—Recordings were made by D. A. McCallum and S. L. L. Gaunt on 29–31 October 1989 and 10–14 May 1991, approximately 80 km N of Songpan, in the mountains of northwest Sichuan Province, People's Republic of China. The "main valley" was visited in both years, a tributary valley (Jiu Zhai Gou National Park) was visited in 1991 only. Both *S. villosa* and, for comparison, the sympatric Eurasian Nuthatch (*S. europaea*) were observed and recorded in conifer forests between 2300 and 2600 m in both valleys. *S. villosa* was also seen at about 2100 m in pine forest in both valleys. *S. europaea* also occurred in *Quercus-Betula* forest in the same elevational range. We recorded vocalizations of at least six *S. villosa* and, for comparison, five *S. europaea,* and heard several others. We did not detect either species at higher elevations in either year, despite approximately two weeks in the field at elevations of 2600–3500 m.

Recordings were made with a Sony TC-D5 Pro II cassette recorder and an Audio-Technica 815A directional microphone, using no parabola, at a tape speed of 4.75 cm/sec. High Bias, CrO_2 recording tape was used. The tapes reside in the collection of the Borror Laboratory of Bioacoustics, The Ohio State University. Recordings were analyzed on a Kay Elemetrics model 5500 digital (DSP) Sona-Graph at a transform size of 100 pts (600 Hz).

Description of vocalizations.—We discerned three basic note-types in recorded vocalizations of *S. villosa.* Type I: harsh, broad-band (3–6 kHz) vocalizations of varying duration (0.23–0.50 msec [N = 14]), repeated at irregular intervals of 0.3 to 1 sec (Fig. 1A, B). The sound is reminiscent of a common ("scold") call of *S. whiteheadi* (Matthysen and McCallum, pers. obs.). Type II: short-duration notes with few or no overtones (Fig. 1C–F); we recorded six variants (IIa–f). All type II notes were 40–65 msec in duration, but they varied in frequency range: 3.2–4.7 kHz (IIa), 2.3–5.3 kHz (IIb), 2.8–4.2 kHz (IIc and IIe), 3.3–4.2 kHz (IId), 3.2–4.2 kHz (IIf). All variants except IIf were recorded in both valleys. Type III: short-duration notes with complex overtones (Fig. 1G). The duration of these notes (mean = 93 msec) was about twice that of type II notes; the frequency range of 2.5–5 kHz was similar to that of the much simpler type IIb variant, but much greater than the other type II variants. Type III notes were recorded in both valleys and in both years.

Type I notes were not grouped in discrete series. Rather they were delivered singly or occurred repeatedly in bouts of vocalizing. They were given spontaneously on occasion (e.g., while a second bird was giving a long series of type II notes), but most type I notes we recorded were given after the observer had stimulated the birds by "squeaking" or "pishing." For example, two birds on 14 May 91 came down from high unseen perches to 2 m above the observer, where they were recorded as they flicked wings and tails while one gave type I notes repeatedly and the other gave "slow song" (see below).

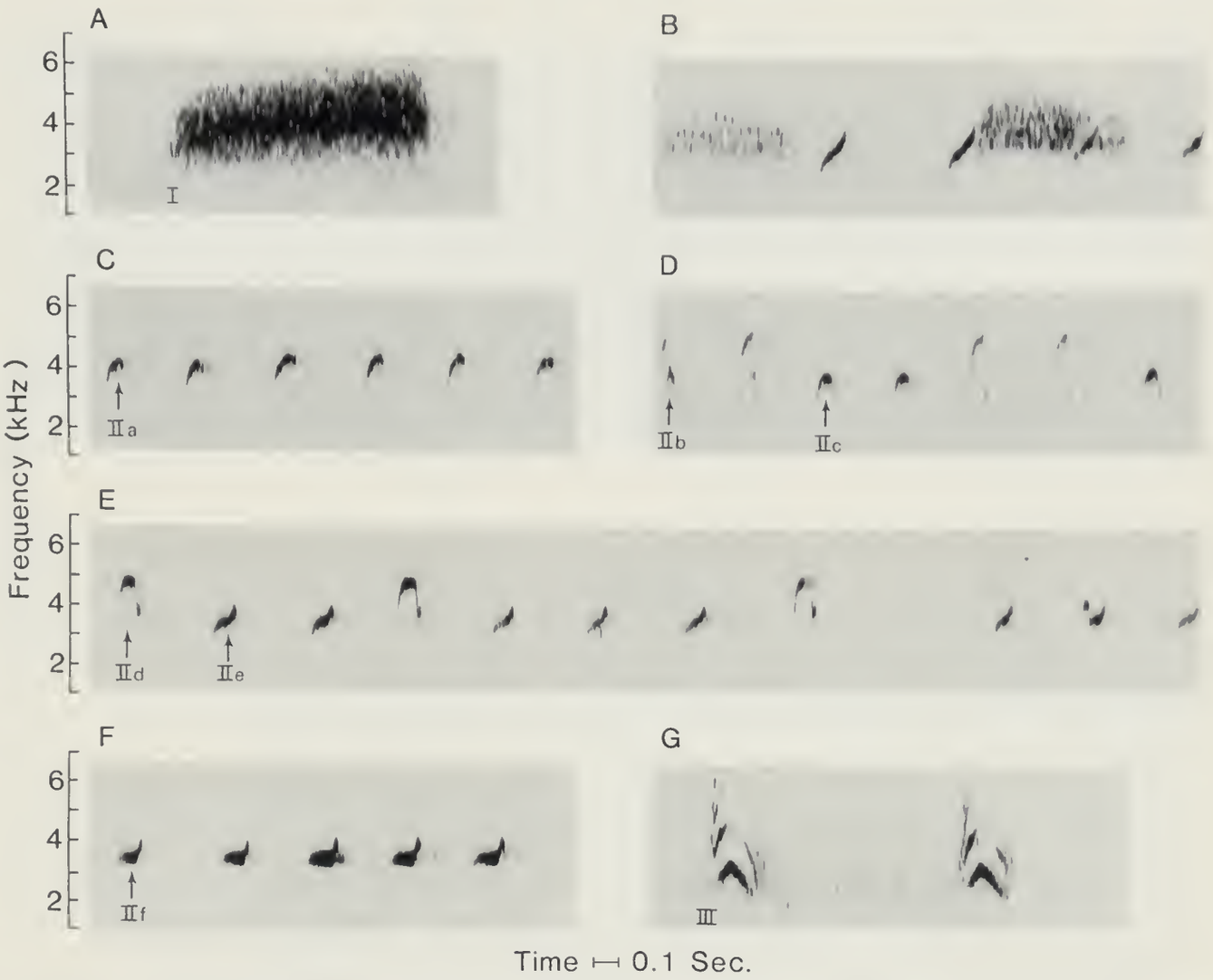

FIG. 1. Sonograms of call notes of the Chinese Nuthatch. A. Type I, single noted, harsh call from recording BLB #17563. B. Harsh call and call type IIe of a second individual, from recording BLB #17563. C–F. Call type II with note types a through f from recording BLB #17423. G. Call type III from recording BLB #17426.

In bouts of vocalizing type II and III notes were combined into multi-note series with patterns that suggest a very simple syntax, as follows: (1) Different note-types are not combined. (2) Variants of type II usually are not combined. (3) Frequency and duration of a given note type or variant does not change noticeably during a single series. (4) Individual series vary markedly in the number and duration of notes. The simplicity of this hypothesized syntax suggests that information is encoded primarily by note type and secondarily by the temporal grouping of notes of a particular type.

Bursts of 5–27 type II notes, separated by intervals of silence roughly equivalent in duration to the bursts were heard and recorded often in spring of 1991 but not at all in autumn of 1989 (Fig. 2). These vocalizations fit the usual conception of "song" (loud, distinct, delivered from high, conspicuous perch). These bursts all possessed an additional syntactical feature: amplitude of the notes increased progressively during at least the first third of the series (crescendo), then levelled off. Notes in "song" series typically were separated by about 100 msec of silence, but one individual increased this interval to 200 msec after coming down from the canopy when the observer "pished." Another individual produced four such "slow songs" of 7–11 type III notes, then gave a long unstructured series of type III notes (see below) before resuming short bursts of type IIe notes.

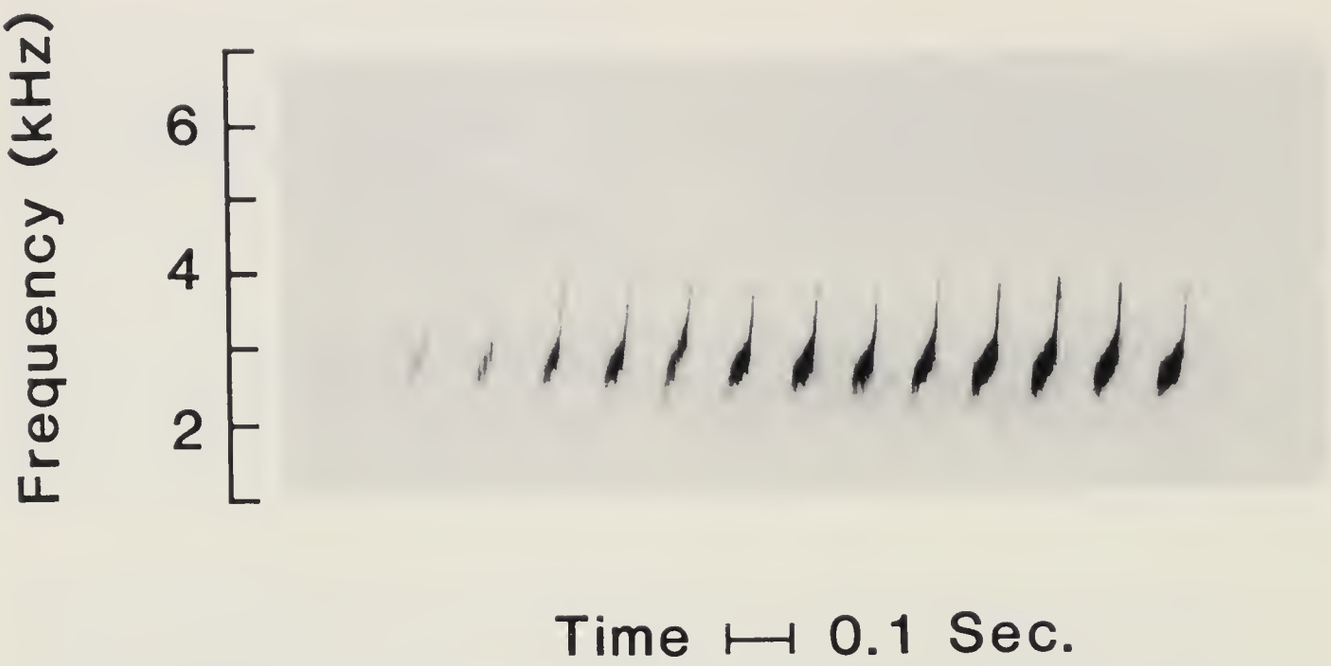

FIG. 2. Sonogram of type IIe notes delivered in a "song" series by the Chinese Nuthatch from recording BLB #17778.

Long series of dozens of type II or type III notes were recorded in spring and autumn. They varied from extremely rapid delivery (inter-note intervals < 100 msec) to irregularly spaced notes with no readily apparent organization. These series were sometimes delivered from treetops, with the bird flicking wings and tail. We detected no clear difference in the demeanor of birds giving these series and those delivering short bursts of notes.

S. europaea produced notes very similar in form to types II and III of *S. villosa* (Fig. 3). We did not detect variants of either type in our small sample. We neither heard nor recorded a type I note from *S. europaea*. *S. europaea*'s syntax appeared identical to *S. villosa*'s, with one additional detail in the case of the short song-like bursts of type II notes. The first note of such a burst was always lower in frequency than those following, and it was flat or rising while the others descended slightly in frequency. Like *S. villosa, S. europaea* produced long series of type II notes and series of widely spaced type III notes, as well as the bursts of "song."

Discussion.—The most striking element in the Chinese Nuthatch's vocal repertoire is the harsh type I note. Similar "scold" calls have been reported in all three Mediterranean nuthatches (Löhrl 1961, Chappuis 1976, Vielliard 1978, Ledant 1978), but not in other nuthatch species, including the superficially similar Red-breasted Nuthatch (*S. canadensis*) of North America (pers. obs.). Our recordings documenting the existence of this call in *S. villosa* provide further evidence for the close phylogenetic relationship of the four species (Voous and van Marle 1953, Vielliard 1978).

Although the harsh "scold" call is the most frequent vocalization, after "song" and low-intensity single "contact" notes, in *S. whiteheadi* (Matthysen, pers. obs.) and *S. ledanti* (Vielliard 1978), this is not the case in *S. villosa*. Chinese Nuthatches used both type II and type III notes in the same contexts as the harsh type I notes. Only type I ("scold") notes have been reported in these contexts for the other three Mediterranean species.

All vocalizations of *S. villosa* resemble those of most other nuthatch species in that they consist of simple notes repeated in series that vary greatly in length and internote intervals (Löhrl 1988). The short bursts of type II notes given by *S. villosa* are similar to the "song" of the Corsican Nuthatch (Matthysen, pers. obs., sonograms in Löhrl 1961 and Chappuis

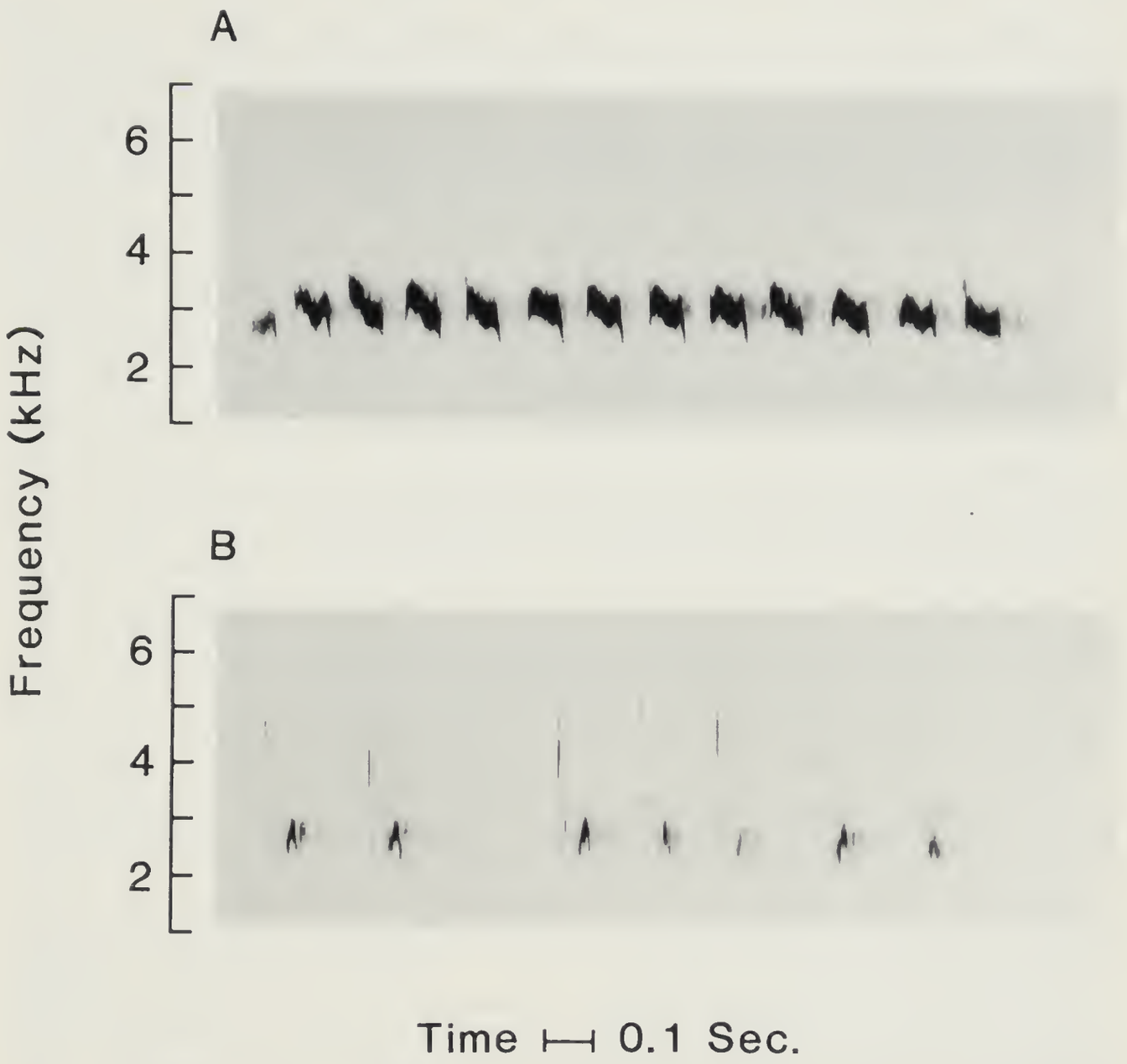

FIG. 3. Sonogram of vocalizations recorded from the Eurasian Nuthatch A. Note type II delivered in "song" series. B. Note type III in call series. Both from recording BLB #17671.

1976) but differ markedly from the "songs" of *S. ledanti* and *S. kruperi* as described by Vielliard (1978).

The Chinese Nuthatch therefore has a full complement of typical *Sitta* vocalizations, as well as the unusual harsh call shared with the Mediterranean group. Vielliard (1978) has interpreted this call as a primitive trait inherited from *Parus*-like ancestors. If that is true, it may be that the typical type II and type III calls (not "songs") have been lost or greatly modified in the Mediterranean species, with the harsh call becoming the most commonly used call. This interpretation is consistent with Vielliard's (1978) contention that the Chinese Nuthatch, with its unique redundancy of call types, is the most primitive member of the genus *Sitta*.

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Bird/ant/acacia symbioses in a mature Neotropical forest.—A variety of avian species nest in swollen-thorn acacias (*Acacia* spp.), presumably because ants symbiotic with the tree afford the birds protection against predators (Janzen 1969, Young et al. 1990). In the ant/acacia obligate symbiosis, ants of the genus *Pseudomyrmex* defend the acacia tree from herbivores and other plants, and the tree produces proteins, lipids, carbohydrates, and specialized thorns for the ants (Janzen 1966).

Parque Nacional Tikal (625 km^2) in northern Guatemala (17°13′N, 89°39′W) is dominated by semi-deciduous tropical dry forest (Smithe and Trimm 1966), which has remained largely undisturbed since ca 900 A.D. White-bellied Wrens (*Uropsila leucogastra*) and Yellow-olive Flycatchers (*Tolmomyias sulphurescens*) are common insectivores in Tikal, both building similar retort-type nests in the understory (Sutton 1948, Skutch 1960), often in swollen-thorn acacias (*Acacia collinsii, A. cornigera,* and *A. gentlei*; Janzen 1974). While both have been noted nesting in acacias (Sutton and Pettingill 1942, Smithe and Trimm 1966, Stiles et al. 1989) this study addresses the selective nature of the nesting association by both the wrens and flycatchers.

To explore the question of nest-site selection, we tested the null hypothesis that the birds nested in acacia trees in proportion to the tree's representation in the forest. During the dry season (February–June 1988), nests were counted and the tree containing the nest noted as acacia or non-acacia. As we were collecting data on a variety of bird and tree species, it is unlikely that our searches were biased for acacias. To estimate the relative density of acacias, circular plots 20 m in diameter were established around four nests (two of each species). Although these plots were chosen for their logistical convenience, they occurred in habitat that appeared representative of the study area. All trees in the plots with at least as many potential nesting sites as the tree chosen by the bird were counted as suitable nesting trees and identified as acacia or non-acacia. We defined suitable nesting trees by the minimum and maximum height of the nests (1.5–15 m) and the range of branch diameters (0.3–2 cm) actually used by the birds. The average relative density of acacias was thereby calculated to be 5.1 ± 1.4% (SD) of the trees available; that is, roughly one suitable nesting tree in twenty was an acacia. Although this method is admittedly inexact, we found it highly conservative; suitable nesting trees often contained many times the number of potential nesting sites as the acacia, but were only counted as one tree.

Based upon this expected frequency, both the White-bellied Wren and the Yellow-olive Flycatcher nested in swollen-thorn acacias more often than would be expected by chance (White-bellied wrens: 55 nests in acacias and four in non-acacias, $\chi^2 = 949.6$, df = 1, $P < 0.001$; Yellow-olive Flycatchers: 27 nests in acacias and 20 in non-acacias, $\chi^2 = 273.5$, df = 1, $P < 0.001$).

The relationship between the birds and the ant/acacia system is likely a commensal one. By protecting the host tree, the ants may inadvertently reduce the bird's risk of nest predation (Janzen 1983:763). The ants could benefit from access to the birds' feces and/or ectoparasites as noted in other bird/insect relationships (Moreau 1942, Chisholm 1952). However, due to the brevity of the bird's nesting periods and their small size, this would appear to be an unlikely source of significant nutrition to the ant colony. Also, we found no evidence of predation on ants by these birds (Janzen 1969). Thus, it seems that the relationship is commensal; the birds receive protection from the ants, whereas the ants and tree are not affected significantly by the birds.

Interestingly, 11 of the 20 Yellow-olive flycatcher nests in non-acacias were within 1 m of a wasp nest (*Polybia*), an association noted by Stiles et al. (1989; see also Wunderle and Pollock 1985). Furthermore, there were three cases in which both flycatcher and wasp nests

occurred in the same acacia. This suggests that nest-site selection in Yellow-olive Flycatchers might be flexible (i.e., in acacias, with wasps, or both) and/or may vary between individuals.

Finally, none of the non-acacia nests of either bird species were located in trees containing thorns. As such trees were common, their non-use could be an indication that the pairs that nest in acacias were selecting for the presence of the ants, not the thorns.

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Vocal responsiveness to chilling in embryonic and neonatal American Coots.—Although neonates of many avian species rapidly develop an ability to thermoregulate physiologically, heat provided by a brooding parent commonly augments the young bird's imperfectly developed endothermic capacity (Theberge and West 1973). Brooding contact between parents and young is stimulated by loud "distress" calls of the young (Gullion 1954, Kirkley and Gessaman 1990). Distress calls, a common response to social isolation, are also stimulated by chilling (Kaufman and Hinde 1961) and may play a role in neonatal temperature control by maintaining parental brooding (Kirkley and Gessaman 1990). Distress calls are also given in response to chilling by late-stage embryos of some species, and so could have a thermoregulatory function before hatching (Evans 1990a). Despite the apparent relevance

of embryonic and neonatal calls for thermoregulation, little is known about the effects of temperature on these calls or how vocal responsiveness to chilling changes with age during the time that thermoregulatory ability is developing. We examined aspects of this problem in the American Coot (*Fulica americana*), a marsh-nesting species in which the newly hatched precocial young commonly are exposed to chilling in air or water but have only a limited endothermic ability (Sutter 1988).

If calls are involved in thermoregulation, we hypothesized that chilling would elicit neonatal calling only at body temperatures below that of young given free access to a heat source and that calling would begin at a body temperature no lower than that at which facultative thermogenesis occurs (approximately 35°C during the first week, Sutter 1988). For embryos at the pipped egg stage, uncorrected chilling could delay hatching (Evans 1990b). We therefore predicted that distress calls would be elicited when late-stage embryos were chilled below normal incubation temperature. Vocal responses due to social isolation or to overheating may also occur (Kaufman and Hinde 1961, Kirkley and Gessaman 1990) but were not examined here.

Methods.—Egg temperatures from the start of pipping onwards were obtained at the Delta Marsh, Manitoba, by replacing one natural egg at each of five nests with an agar-filled egg having thermal characteristics similar to a fresh egg (Evans 1989). The artificial eggs were never rejected by the parents and appeared to be incubated normally. The egg at one nest was fitted with a calibrated temperature-sensitive transmitter (Minimitter model L) monitored with a remote receiver. The other four eggs were fitted with implanted thermistor probes wired to remote, calibrated temperature recorders (YSI and Grant Instruments Cambridge). Readings were taken at intervals of from 15 min to 1 h. All readings for a given nest were averaged, providing one data point per nest for subsequent analysis.

Eggs for laboratory study were incubated in a commercial incubator held at 37.8 ± 0.5°C and 60 ± 5% relative humidity. Young were group-reared in pens providing moistened commercial chick starter, water, and access to an incandescent heat lamp. Pipped eggs and young were chilled by individually placing them within a coil of copper tubing through which water at either the control (37.8°C) or cold (20.0°C) temperature was pumped from controlled water baths (see Evans 1990a for details of apparatus). Calls/min were counted with a sound-operated relay and event recorder. Coot embryos within pipped eggs, like newly hatched young, emit a graded series of calls ranging from soft contentment "twitters" to loud "distress" calls (Cosens 1981). The intensity setting of the relay was chosen by trial and error to achieve maximum separation between these calls so that only loud distress calls were recorded. Body temperatures at the end of each minute were obtained with a 0.4-mm diameter flexible thermocouple inserted about 1 cm into the cloaca of chicks or into the pip hole of pipped eggs. Temperatures were measured to the nearest 0.1°C with a Sensortek model Batt-12 thermometer.

Testing began with a 10-min pre-test at control temperature (37.8°C) to establish baseline vocal response levels. Water at the experimental temperature (20.0°C) was then pumped through the coil for 30 min. Chilling was followed by a 10-min post-test at the control temperature. Eight embryos were tested during the final day before hatching, when pip holes were well developed. Young were tested on the day of hatching (day 0, N = 9), day 3 (N = 12) and day 7 (N = 11). Pipped eggs and young were selected for testing on the basis of availability at the appropriate age, without reference to their use in tests at an earlier age. This procedure minimized the number of eggs collected while maintaining statistical independence of individuals within age classes. Preliminary analyses indicated that there were no effects ($P > 0.5$) of prior testing. Statistical comparisons of paired measures on each individual within age classes employed either Paired-*t* or, for non-normal data, non-parametric Wilcoxon matched pairs tests (Sokal and Rohlf 1969).

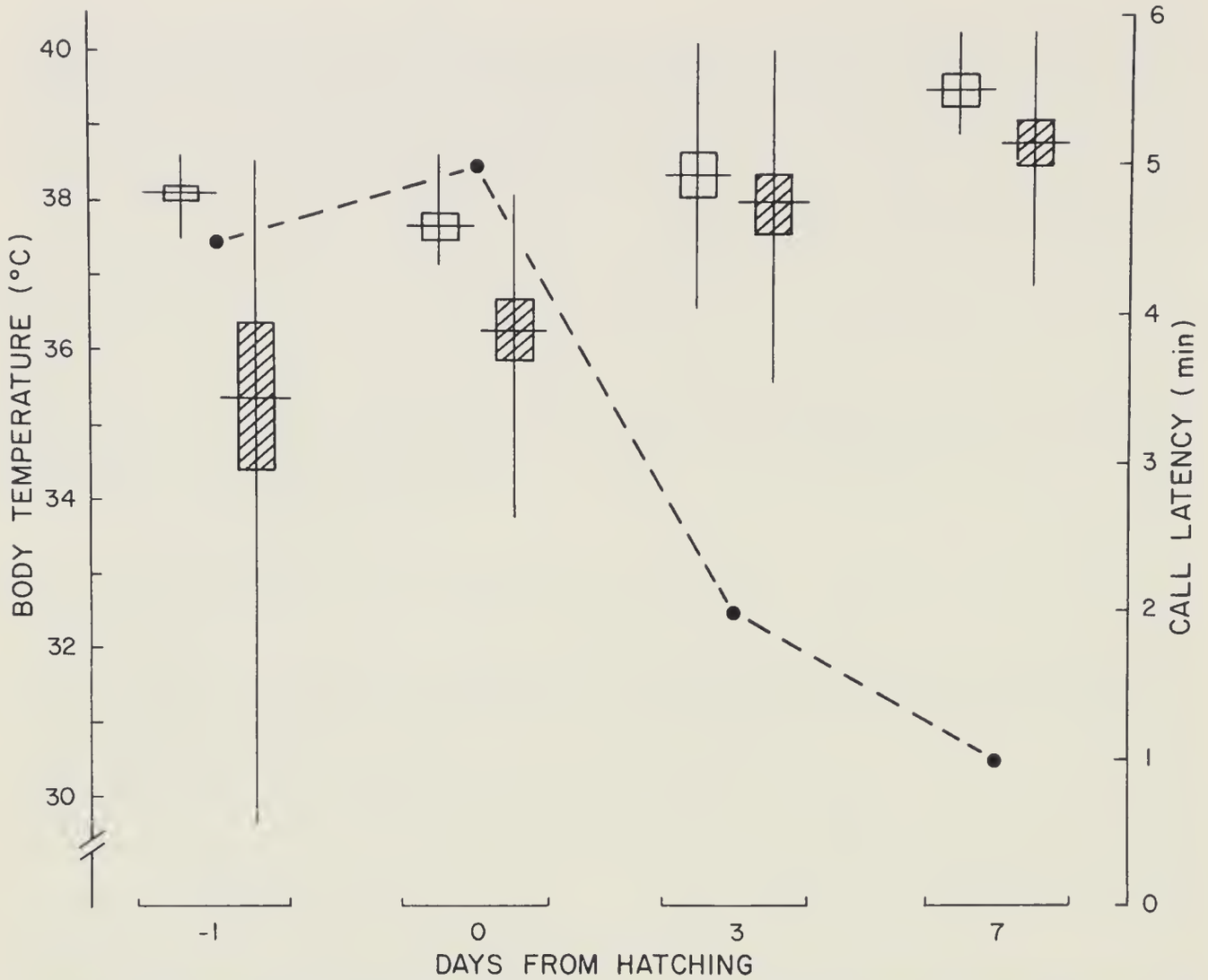

FIG. 1. Effects of chilling on body temperature and time to start calling (latency) in embryos at the pipped egg stage (−1 day), in young on the day of hatching (0 days), and at three and seven days of age. Body temperatures shown by horizontal lines (mean), bars (±SE) and vertical lines (range). Open bars = last minute at control temperature before chilling started; hatched bars = minute during which calling began after onset of chilling. Solid circles and dashed lines indicate median time to begin calling after the onset of chilling.

Results.—An average of 148 ± 41 (SE) readings were taken at the five naturally incubated nests. Mean temperature was 35.0 ± 0.5°C (range = 33.9–36.0°C). During the pre-test period in the laboratory, body temperatures of pipped eggs and young at zero and three days of age were similar to the control incubation temperature of 37.8°C. Pre-test temperatures were about 1.5°C higher at seven days of age (Fig. 1, Table 1). During subsequent chilling, body temperature dropped steadily for all ages, reaching a mean of from 27.1°C for eggs to 35.0°C for seven-day-old young by the final minute (Table 1). There was at all ages a small but significant drop in body temperature between the final test minute and the first post-test minute at the warmer control temperature (Table 1). Body temperature then increased gradually throughout the remainder of the post-test period.

At each age, modal and median pre-test call rates were zero. During subsequent chilling, median time to begin calling (defined as the first minute in which at least five calls were given) was about five min for pipped eggs and newly hatched young, followed by a decrease down to one min by seven days of age (Fig. 1). Once calling began, it usually continued unabated until after the end of chilling at all ages. Embryos at the pipped egg stage began

TABLE 1

EFFECTS OF REWARMING CHILLED EMBRYOS AND YOUNG ON MEDIAN CALLS AND MEAN ± SE BODY TEMPERATURE (SAMPLE SIZES IN PARENTHESES)

Period (min)	Pipped eggs (8)		Hatch day (9)		Three days (12)		Seven days (11)	
	Calls[a]	T_b[b]	Calls	T_b	Calls	T_b	Calls	T_b
Pre-test	0	38.1 ± 0.1	0	37.7 ± 0.2	0	38.4 ± 0.3	0	39.5 ± 0.2
Test: final	13	27.1 ± 0.2	21	30.4 ± 0.3	24	31.7 ± 0.5	25	35.0 ± 0.3
Post-test: 1	1.5	26.9 ± 0.2	11	30.1 ± 0.3	9	31.5 ± 0.5	9	34.8 ± 0.3
3	0	27.4 ± 0.2	0	30.6 ± 0.3	0	32.0 ± 0.5	1	35.1 ± 0.2
5	0	27.9 ± 0.2	0	31.3 ± 0.3	0	32.6 ± 0.5	0	35.5 ± 0.3
Statistic[c]	T = 0, t = 2.75		T = 3, t = 8.03		T = 0, t = 8.96		T = 1, t = 6.38	
P	<0.05	<0.02	<0.02	<0.001	<0.01	<0.001	<0.01	<0.001

[a] Per minute.
[b] T_b = body temperature (°C).
[c] Comparisons between final test minute and first post-test minute. T = Wilcoxon matched-pairs test, t = paired t-test.

calling only after their body temperature had dropped significantly below pre-test levels (Fig. 1, Paired $t = 2.49$, $P < 0.05$) to a level that did not differ significantly (unpaired $t = 0.19$, $P > 0.5$) from the mean natural incubation temperature of 35.0°C. Body temperature at the time calling began increased with age but was still significantly lower than pre-test levels in newly hatched young (Paired $t = 3.66$, $P < 0.01$). By three and seven days of age (Fig. 1), calling began when there was only a slight ($P > 0.05$) decrease in body temperature from pre-test levels.

There were significantly fewer calls given during the first post-test minute of rewarming than during the final minute of testing despite the continuing drop in deep body temperature at that time (Table 1). By the third post-test minute, median call rate had dropped to zero at all ages except seven days, where median rate was one call per min. Median call rate was zero for all ages by five min post-test.

Discussion.—The results support our prediction that calls of late-stage embryos would be stimulated at body temperatures below normal incubation temperature. We did not anticipate that calling would begin at, rather than below, incubation temperature, since such a response would appear to serve little or no thermoregulatory function. However, this unanticipated result may be more apparent than real. It is likely that the embryonic temperature of live pipped eggs during natural incubation would be slightly above the temperature we recorded in our artificial eggs (Drent 1970), thereby bringing the laboratory results into closer agreement with functional expectations. Calling by young coots occurred at temperatures above that at which facultative thermogenesis occurs (about 35°C, Sutter 1988). This sensitivity, if present under natural conditions, should enhance the thermoregulatory effectiveness of distress calling. Our prediction that young should call only after body temperature decreased below the level that they could maintain when given free access to a heat source was supported by hatch-day young but only marginally by older young. By three and seven days after hatching, the young were so sensitive to chilling that calling began when there was only a slight, nonsignificant drop in deep body temperature.

The rapid cessation of calling during the first post-test minute despite the continuing decline in deep body temperature at that time (Table 1) suggests that peripheral receptors are involved in cessation of calling. Peripheral receptors are known to be involved in the cessation of other thermoregulatory activities in birds (Bligh 1973). In the wild, the onset of warming after chilling would normally indicate that corrective parental action had been taken, thereby removing the need to continue calling even before deep body temperature had begun to increase.

Vocal responsiveness to chilling is the only thermoregulatory mechanism able to function while the embryo is trapped within the confines of the pipped egg. On the day of hatching, a strong vocal response to chilling still occurs, but movement of the young to a heat source becomes a more sensitive mechanism for maintaining core temperature. By the age of 3–7 days, vocalizing and movement appear to be equally sensitive to chilling, and both have a higher temperature threshold than facultative thermogenesis. Although it remains to be proven that calling to the parent is involved in coot thermoregulation, the sensitivity of the response to chilling indicates that it would be highly efficient in that capacity.

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Successful exchange of prairie-chicken eggs between nests in two remnant populations.— Declining fecundity may be a classic symptom of inbreeding depression, and is expected in isolated populations that have fallen below about 50 individuals (Franklin 1980, Shaffer 1981, Simberloff 1982, Brussard 1985). Sterility of males was suspected as a contributing factor in the extinction of the Heath Hen (*Tympanuchus c. cupido*) (Gross 1928). Currently, each of the three remaining populations of Greater Prairie-Chickens (*T. c. pinnatus*) in Illinois contains fewer than 50 individuals, and 28 years (1963–1990) of nest data for the Jasper County population show significant declines in egg fertility and egg success (hatched eggs/total eggs) (Westemeier, unpubl. data). The number of Illinois prairie-chickens declined from millions throughout the state about 1860 to estimates of 25,000, 2000, 500, and 76 in increasingly scattered population in 1933, 1962, 1972, and 1990, respectively (Westemeier 1985, unpubl. data).

Following a joint decision by the Illinois Dept. of Conservation (IDOC), Illinois Natural History Survey (INHS), Illinois Nature Preserves Commission, and Illinois Endangered Species Protection Board to address possible inbreeding depression in Illinois prairie-chickens, an effort was undertaken in 1990 to exchange clutches of eggs under incubation in Jasper and Marion counties. The objective was to enhance genetic variation in both gene pools by mimicking natural dispersal. The two populations, about 56 km apart, are supported by a total of 858 ha of intensively managed sanctuaries. Except for one intervening lek with four males in spring 1990, about 42 km from the Jasper population, former lek sites between

the two managed populations have not been used for 14–25 years. Movements by prairie-chickens of 42–56 km, and more, are possible (Hamerstrom and Hamerstrom 1973), but current exchanges of genetic material are unlikely in Illinois.

This paper describes what we believe is a first attempt to exchange eggs between prairie-chicken nests. An exchange of grown birds between the two populations was deemed unlikely to succeed because of the large numbers needed, the probability of high dispersal and mortality, and difficult logistics (Toepfer 1988, Moe 1990).

To find one or more prairie-chicken nests of reasonably synchronized incubation in each population, three teams (of four to six searchers each) searched 146 ha of sanctuary grasslands between 25 April and 31 May 1990 (86 person-days). Searchers walked side by side, each viewing a 1.5-m swath and using a 1.5-m staff to carefully part vegetation to view possible nest sites (Westemeier and Buhnerkempe 1983). The risk of stepping on active nests was lessened, where possible, by each nest searcher walking in wheel tracks made in grasslands the previous summer or fall by combines, which harvested grass seed, or by tractors, which pulled mowers. Estimates of the stages of incubation were made by submerging three eggs of each clutch in water (Westerskov 1950). When incubating hens were flushed off their clutches, search teams promptly left the sanctuary areas to allow for a quick return by hens. To reduce the risk of desertion and predation, nests were not revisited until clutches were believed to be within one week of hatching (incubation period = 25 ± 2 days [Silvy 1968, McEwen et al. 1969, Svedarsky 1979]). Ages of prairie-chicken embryos were estimated by making slight adjustments of criteria for Ring-necked Pheasant (*Phasianus colchicus*) embryos which hatch in 23 days (Labisky and Opsahl 1958).

Among seven prairie-chicken nests located in Jasper County and three in Marion County, two clutches were estimated potentially synchronous in that incubation had not started. In Jasper County on 25 April, a hen flushed from a 10-egg clutch when searchers were about 10 m from the nest. In one Marion County nest on 27 April, no hen was present at a clutch of 12 eggs. Both nests were in fields of smooth brome (*Bromus inermis*), which largely concealed both nests.

On 18 May 1990 at 07:30 h CST, we made simultaneous checks of the two experimental nests. Both clutches were being incubated. The hen at the Jasper County nest flushed when the examiner was still 5 m from her nest. Of the 10 eggs still present, two were estimated to be at 16 days of incubation, one was estimated to be either at 23 days of incubation or addled, and the remaining seven eggs were not checked. In contrast to the hen at the Jasper nest, the hen at the Marion County nest jumped aggressively at the examiner's searching stick from a clutch of 15 eggs and then ran off in a wheel track. A check of three eggs in the Marion nest indicated about 16 days of incubation. While an observer remained about 30 m from each nest (to avoid repeated flushing of hens), the other team members made a decision by telephone to proceed with the egg exchange. At 08:00 h, the eggs were removed from each nest and substituted with warm pheasant eggs. This substitution was made in case either hen returned to her nest unseen by the nearby observers. During the transfer, eggs were kept warm by each vehicle's heater. At 09:00 h, the pheasant eggs were removed and the exchange of prairie-chicken eggs was completed in each nest. Neither hen was observed during the 1.5 h required to make the exchange. Temperatures from 07:30–12:00 h ranged from 11 to 23°C, respectively; winds, from calm to 6 km/h; and skies, from clear to partly cloudy.

On 23 May, one egg, withheld from the Marion County nest for genetic studies and for a more accurate determination of incubation stage, hatched in an incubator by 08:15 h. At 11:45 h on the same day, the Jasper County nest, which contained 14 eggs from the Marion County clutch, was observed to be successful, with the chicks ready to leave the nest. This time the hen at the Jasper County nest flushed about 3 m from the examiner. A final check

of the Jasper County nest on 29 May revealed that 12 of 14 eggs had hatched; two intact eggs contained embryos that had died at about six and 24 days of incubation. The Marion County nest, which contained 10 eggs from the Jasper nest, was also successful by 29 May: eight eggs had hatched (exact date unknown); one intact egg contained a dead, 10-day embryo; and another intact egg was addled and showed no sign of a germinal disc or embryo.

Thus, the three dead embryos died six to nine days before, and eight days after, the day the exchange was made, so no mortality was attributable to the exchange. The hatching rate was in fact lower for seven clutches not exchanged (45%) than that of the two exchanged clutches (84%) ($\chi^2 = 6.112$, df = 1, $P < 0.02$). For 112 eggs not exchanged, 11 were missing, 32 were infertile, 50 had hatched, and 19 contained dead embryos whose deaths were unattributable to researcher activities. The missing eggs may have resulted from partial depredation in three clutches or from the breaking of rotten eggs which then stuck to the hens' feathers and brood patches and were carried off inadvertently. One hen extended her incubation period to ≥35 days before her 16 rotten and apparently sterile eggs began to break under her. Although such attentiveness indicates a prairie-chicken will extend her incubation period, the physiological costs of such an extension may jeopardize her survival or that of her brood. We believe the stages of incubation for clutches considered for an exchange should be in close synchrony.

This project demonstrated the tenacity of incubating prairie-chickens and, thus, the feasibility of exchanging eggs between clutches. Prairie-chickens readily accept a sudden change in clutch size, eggs from different members of their own species, or pheasant eggs among their eggs (Westemeier 1988). The technique described here offers hope for enhancing genetic variability. If some of the young from the egg exchange ultimately breed, increased heterozygosity in the two populations may be achieved.

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Occurrence of the Andean Condor in the Perijá Mountains of Venezuela.—The occurrence of the Andean Condor (*Vultur gryphus*) in Venezuela was first documented by two specimens now in the British Museum which were collected near the city of Mérida (Fig. 1); the most recent was a juvenile taken ca 1912 by Briceño Gabaldón (Swann 1921; Phelps and Phelps, Jr. 1958). Since then, this rare species was thought to be extinct in Venezuela (Phelps, Jr. and Meyer de Schauensee 1979), and Alden (1975) recommended excluding it as occurring in the country. However, on 7 July 1976, Zonfrillo (1977) observed three condors along the road from Mérida to Jají: one near the waterfall at La Chorrera, 30 km from Mérida, and two adults (one male) three km nearer Jají. The area appeared to be good nesting habitat, but no signs of nesting were seen. The birds were considered visitors from the Santa Marta or Andes mountains of Colombia, the nearest known condor breeding localities (Hilty and Brown 1986).

Since 1976, there have been no more sightings near Mérida, and the status of the condor still remains uncertain in Venezuela and in other countries of the Andes Mountains where it is considered in danger of extinction (USFWS 1986). Indeed, in Venezuela and Colombia, few regions seem to remain appropriate for this species due to human intervention, except the high Perijá Mountains that form the frontier between the two countries. It was here, on 27 August 1985 that Leonel Lanier, a mountain climber, ascended to the Páramo of Tetari and observed a condor flying above Torote-jopa Peak (in Venezuela) at an elevation of 3225 m, between 11:00 and 15:00 h. Again in 1986, Lanier conducted an expedition to the Páramo

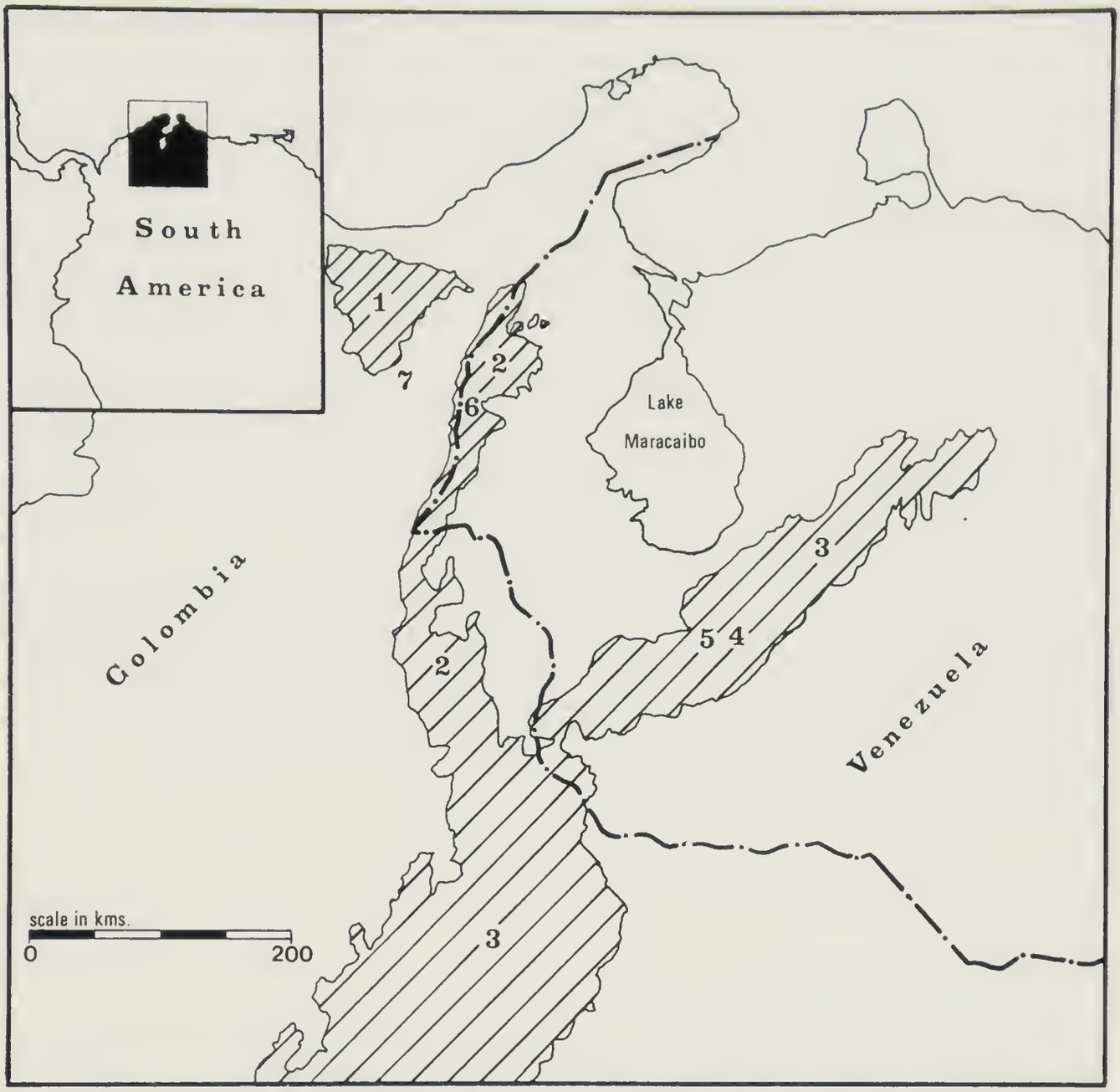

FIG. 1. Map of western Venezuela and adjacent Colombia showing the position of the (1) Sierra Nevada of Santa Marta, (2) Perijá Mountains, (3) Eastern Andes Mountains of Colombia and Venezuela, (4) Mérida, (5) Jají, (6) Páramo of Tetari and Cerro Pintado, and (7) Valledupar. Only mountains above 1000 m are shown.

of Tetari to 3600 m, where he saw a condor resting on a cliff ledge of Torote-jopa Peak on 23 July. Another condor (same bird?) flew over the Páramo on 24 July.

To verify Lanier's sightings, one of the authors (Viloria) ascended to this little known Páramo on 30 Oct. 1989 and at ca 15:30 h observed two adult condors gliding in a circle over the campsite at the base of Rafael Urdaneta Peak (in Venezuela) at 3440 m. Afterwards, the birds flew northward until out of sight. Again, at 18:00 h, a condor passed over the campsite flying southward. On 31 October the weather was foggy, but one condor was observed flying over Tetari Peak, ca 10:00 h.

The high Perijá Mountains, especially the Páramo of Tetari, are appropriate habitat for the condor. There are steep rocky cliffs, deep canyons, and even rocky shelters and caves preferred by this species for nesting and roosting. Human intervention is minimal. Deer

(*Mazama* sp.), rabbits (*Sylvilagus* sp.), and pacas (*Agouti taczanowskii*) are present and could serve as food. There are no domestic animals present such as cattle or goats. A visit was made to the Páramo of Cerro Pintado (ca 3200 m) for three days in March 1989, but no condors were seen. The habitat appeared appropriate, but there was much agricultural activity such as cattle grazing and vegetation burning. However the authors believe Cerro Pintado is within the condor's territory because it is only 22 km north of Tetari Peak, an insignificant distance for a large soaring bird. Also, since condors have been reported from the nearby locality of Valledupar, Colombia (Hilty and Brown 1986), birds in Perijá may fly to and from the Sierra Nevada of Santa Marta only 60 km away (Hilty and Brown 1986, Norton 1975).

Perhaps these birds are recent arrivals from Santa Marta, where human disturbance has been increasing, or have always been present in this unexplored area. Successive sightings of Andean Condors in 1985, 1986, and 1989 in the Páramo of Tetari indicate they may be resident. It is noteworthy that no more than three condors have been seen in any one place. Fortunately, the Páramo of Tetari (mostly within Venezuela) is part of the Perijá National Park decreed by the Venezuelan government in 1978.

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This note is the first report of the Páramo of Tetari Expedition, undertaken in 1989 by the Biology Museum of the Univ. of Zulia.

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Distribution and population status of Harlequin Ducks in Idaho.—Harlequin Ducks (*Histrionicus histrionicus*) occur in two distinct populations in North America. The population wintering along the northern Atlantic coast has declined substantially (Goudie 1989) to about 1000 individuals and is currently listed as endangered in eastern Canada. The population wintering along the northern Pacific coast is much larger (Bellrose 1980), although population size and trend are unknown. Harlequin Ducks migrate inland to nest along swiftly flowing mountain streams (Bellrose 1980). In Idaho, they are considered uncommon summer residents in the northern part of the state (Burleigh 1972). Although the AOU check-list (1983) reports that Harlequin Ducks breed from the Canadian border south to central Idaho, we found only one Idaho breeding record (Hand 1941) and four sight records (Merrill 1897; Rust 1915; Hand 1932, 1941) in published literature. Due to their apparent scarcity in Idaho, Harlequin Ducks were classified as a "sensitive species" by Regions 1 and 4 of the U.S. Forest Service in 1987 and 1990, respectively, and a species of spécial concern by the state in 1989 (Moseley and Groves 1990). From 1987–1990, we conducted surveys to determine distribution, population status, habitat use, and breeding biology.

Methods.—We surveyed 75 mountain streams in northern, north-central, and southeastern Idaho between April and August, 1987–1990, for Harlequin Ducks. Streams were selected for survey based on the availability of suitable habitat (Wallen 1987), personal knowledge or reports of Harlequin Duck use, and proximity to streams known to be used by Harlequin Ducks. Surveys were conducted by hiking, rafting, inner-tubing, or driving along streams. Most streams were surveyed several times in at least two of the four years. We also distributed a poster statewide requesting information on sightings of Harlequin Ducks. Below we include results of our own field surveys and reports from U.S. Forest Service biologists, state fish and game biologists, and other experienced observers made between May and September 1987–1990.

Results and discussion.—We observed adult Harlequin Ducks on 16 streams and broods on eight of those streams; we received reports of adults on 17 additional streams and broods on five other streams. Population densities on stream reaches used by Harlequin Ducks averaged 0.15 pairs/km of stream. The majority of streams (73%) where Harlequin Ducks were sighted and all streams where broods were observed are located between the Lochsa River (46°30′N, 114°57′E) in north-central Idaho and the upper Priest River (48°58′N, 115°56′E) near the Canadian border.

In northern and north-central Idaho, Harlequin Ducks were observed at elevations from 600 to 1200 m. These streams were usually associated with riparian habitat dominated by an overstory of western red cedar (*Thuja plicata*) or western hemlock (*Tsuga heterophylla*). In southeastern Idaho, Harlequin Ducks were observed from 1770 to 1890 m in elevation with riparian habitat dominated by shrubs (*Salix* spp.) and a canopy of Douglas-fir (*Pseudotsuga menziesii*). Although breeding has not been confirmed in southeastern Idaho, breeding does occur just across the border in northwestern Wyoming.

Harlequin Ducks are relatively unproductive, in part due to a high nonbreeding rate (Bengston 1972, Kuchel 1977, Wallen 1987), and not all streams where breeding occurs produce broods every year. Therefore, breeding may be occurring on some streams where we observed only adults. However, other streams are probably only used during migration between coastal wintering areas and breeding areas farther east in Wyoming and Montana (Wallen and Groves, unpubl. data). Early spring observations and observations of adults in mid- to late-summer in particular may be of migrating ducks. Thus, a breeding distribution based upon the presence of pairs on streams during early spring or of single birds later in the season can overestimate actual breeding range.

Our surveys indicate that only a small number of Harlequin Ducks breed successfully in Idaho. We observed 32 pairs in 1990, and only about a third (11) of those pairs produced broods. We estimate that the adult population resident in Idaho during the breeding season is less than 100 individuals, distributed primarily on 28 streams over approximately 38,000 km^2 in northern and north-central Idaho.

As Goudie (1989) noted, the Harlequin Duck has received little scientific attention, and there are few data to compare our population estimates historically either in Idaho or elsewhere. Although Harlequin Duck breeding surveys are currently being conducted in Montana (D. Genter, pers. comm.) and western Washington (G. Schirato, pers. comm.), almost nothing is known of their breeding status in adjacent Oregon (K. Durbin, pers. comm.) or British Columbia (W. Campbell, pers. comm.). Densities of Harlequin Ducks on streams in Grand Teton National Park, Wyoming (Wallen 1987), Glacier National Park, Montana (Kuchel 1977), and Iceland (Bengston 1972) are higher than those in Idaho, while densities in Labrador are considerably lower (Goudie 1988).

Goudie (1989) cited evidence that hunting of Harlequin Ducks may have been responsible for declines in eastern North America. However, further investigation into factors limiting Harlequin Duck populations is warranted. Conservation of nesting and brood-rearing habitat along streams where they breed may be critical to their continued existence in Idaho and elsewhere.

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House Sparrows open an automatic door.—House Sparrows (*Passer domesticus*) are notable for their behavioral plasticity. We here report a remarkably novel manifestation of House Sparrow behavioral adaptability.

On the morning of 29 December 1990, we saw House Sparrows repeatedly opening an automatic sliding door on the outside of the Hamilton, New Zealand, Intercity Bus Station. The Horizon® automatic door consisted of two glass panes, each ca 1.2 m in width, designed so that one slides past the other. The door connected a waiting room and small cafe with the bus platforms outside. Above the sliding door on both the inner and outer walls was mounted a small sensor, shaped like a rectangular box, slanted downward toward the space in front of the door to be triggered effectively by persons wishing to pass through. A small green light shone continuously from the front of the sensor, and an equally small red light shone twice for < one sec duration, separated by a one sec interval, when movement in front of the door was sensed. The top surface of both sensors (ca 4 × 10 cm) was covered with small bird droppings.

At least two males, but no females, employed similar techniques to cause the door to slide open. A bird either flew slowly past the sensor, at a distance of <10 cm, or hovered briefly in front of the sensor at a similar distance, or landed on top of the sensor, leaned forward, and bent its neck until its head triggered the sensor and the door opened. After a pause of one to several sec, the bird then flew through the doorway. In about 45 min of observations (30 min from ca 07:00 to 07:30 and 15 min from 10:00 to 10:15), we saw sparrows open this door 16 times. A short return visit in the afternoon of the same day revealed several more instances. Female sparrows simply waited for persons to open the door for them, then flew through the doorway behind the person before the door slid shut. Occasionally, a female sparrow perched on the floor of the waiting room or on the tarmac outside, ca 2–3 m from the door, and appeared to wait for a person to activate the door. Male sparrows sometimes did the same.

The traffic supervisor, J. Price, informed us that the door had been installed only two months previously (there are still swinging doors at both ends of the sliding door). He was aware that sparrows had been opening the door and noted that they had learned this "very quickly" after the door had been installed.

There would seem to be at least two factors contributing to the learning of this remarkable behavior. Sparrows are tolerated around cafe tables in the bus station, as is true in similar circumstances throughout New Zealand. Indeed, they are certainly rewarded for their predisposition to scavenge crumbs from table tops and the floor beneath tables. Hence, there were both food rewards and time without persecution available to them inside the waiting

room's cafe. Sparrows had been flying through the open swinging doors before the sliding door was installed.

There are at least two possible ways by which door-opening behavior could have been learned by sparrows. First, the flashing red light may have become associated with the door sliding open and attracted a sparrow to the sensor. Then, random movement would have yielded the reward, and perhaps a single sparrow learned the association between its position in front of the sensor and the opening of the door. Alternatively, the sensor may have been approached simply as an appropriate, convenient perch. Once again, random movement may have then led to activation of the door and associative learning. Other sparrows may well have acquired the door-opening behavior through observational learning.

Early research (Porter, Am. J. Psychol. 15:313–346, 1904, Am. J. Psychol. 17:248–271, 1906) on the problem-solving abilities of sparrows included mention of sparrow persistence in solving problems in the laboratory, compared to other species of birds tested. Summers-Smith (The House Sparrow, Collins, 1963) emphasized the behavioral plasticity of sparrows and provided anecdotes of innovative behavior. He noted several aspects of the biology of House Sparrows that may contribute to the species' colonizing success. These include acceptance of a wide range of foods, tolerance of human proximity and disturbance, and general adaptability in possible nest sites.

It is somewhat surprising that problem-solving and behavioral plasticity in House Sparrows has not received more attention, considering the obvious success of sparrows as colonizers. We reiterate the emphases of Porter and Summers-Smith and suggest that additional research on learning and problem-solving by House Sparrows may further elucidate behavioral mechanisms contributing to the species' success.

Acknowledgments.—We thank P. Gowaty, T. Lee, and two anonymous reviewers for comments on this manuscript. Travel costs of RB were partially funded by a grant from the Center for International Studies, Univ. of Dayton.

Randall Breitwisch and Margaret Breitwisch, *Dept. of Biology, Univ. of Dayton, 300 College Park, Dayton, Ohio 45469-2320.* *Received 30 April 1991, accepted 1 July 1991.*

Wilson Bull., 103(4), 1991, pp. 727–743

PROCEEDINGS OF THE SEVENTY-SECOND ANNUAL MEETING

JOHN L. ZIMMERMAN, SECRETARY

The Seventy-second Annual Meeting of the Wilson Ornithological Society was held Wednesday, 15 May to Sunday, 19 May 1991, at the University of Oklahoma, Norman, Oklahoma, in joint session with the Cooper Ornithological Society. The local committee chaired by Dr. Gary D. Schnell was composed of Wendy Anderson, Ruth H. Boyd, Patricia Bergey, Neil J. Buckley, Janet K. Braun, Victoria J. Byre, Brian R. Chapman, Holly H. Edwards, James R. Fish, Rick Fry, Joseph A. Grzybowski, Melynda Hickman, Daniel J. Hough, William R. Johnson, Timothy C. Lamey, Douglas W. Mock, Pam A. Pogorelc, Darrell W. Pogue, Coleen Cassady St. Clair, Christine E. Skelly, Steven K. Shore, Mark Snively, Peter B. Tirrell, Linda E. Watson, and Marsha K. Womack. The meeting was hosted by the Department of Zoology, Oklahoma Biological Survey, and Oklahoma Museum of Natural History, all of the University of Oklahoma, and the Cleveland County Audubon Society and the Oklahoma Ornithological Society. Other supporters included an anonymous donor, Oklahoma City Zoo, Office of Research Administration and the College of Arts and Sciences of the University of Oklahoma, University of Oklahoma Foundation, University of Oklahoma Press, and University of Texas Press.

The Council met from 13:09 to 21:00 on Wednesday, while registration for the 197 guests and members began in the Forum Building of the Oklahoma Center for Continuing Education. A joint dinner with the Cooper Society Board and the Wilson Society Council was held in the President's Dining Room of the OCCE Commons Restaurant, followed by a "very informal social hour" sponsored by the Cleveland County Audubon Society. The opening session on Thursday convened in the Forum Room of the Oklahoma Center for Continuing Education where the Society was welcomed by Dr. Eddie C. Smith, Vice Provost for Research Administration, Univ. of Oklahoma. President Jared Verner responded for the Cooper Ornithological Society and, President Jon C. Barlow responded for the Wilson Ornithological Society.

The scientific papers sessions, which included contributed papers and symposia on the Interface of Science and Conservation, convened by Mercedes S. Foster and Richard C. Banks, and on Endangered Passerines, convened by Joseph A. Grzybowski, were held in the Forum Building. Poster papers were presented in corridor B of the Forum Building and were highlighted by an informal social Friday evening following an outdoor barbecue on the OCCE grounds for which the Oklahoma Ornithological Society provided additional refreshments. Field trips to local areas were conducted by The Cleveland County Audubon Society on Thursday, Friday, and Saturday mornings. Sunday trips included a trip to the Wichita Mountains National Wildlife Refuge near Lawton and extended opportunities for birding in the Oklahoma City-Norman area. During the meeting, guest tours were provided by the local committee to Myriad Gardens, United Design Corporation and the Rose Rock Museum, and the Oklahoma City Zoo.

The annual banquet was held in the Commons Restaurant of the OCCE Center, preceded by a social hour sponsored by the University of Oklahoma. After the banquet the following awards were presented:

EDWARDS PRIZE (for the best major article in volume 102 of *The Wilson Bulletin*) to

Keith L. Bildstein, William Post, James Johnston, and Peter Frederick. "Freshwater wetlands, rainfall, and the breeding ecology of White Ibises in coastal South Carolina." Wilson Bulletin 102:84–98.

LOUIS AGASSIZ FUERTES AWARD

Daniel A. Cristol, "An experimental test of the arrival-time hypothesis of differential migration."

MARGARET MORSE NICE AWARD

James R. McCammon, "Reduction of bird fatalities during nocturnal migration."

PAUL A. STEWART AWARDS

Daniel R. Koslovic, "Host selection in a generalist brood parasite—interaction between the Brown-headed Cowbird and House Finch."
Robert A. Mauk, "Population dynamics and demography—Leach's Storm-Petrel on Kent Island, New Brunswick, Canada 1953–90."
Stuart M. Slattery, "Effect of overgrazing on gosling growth and survival in Ross' and Lesser Snow Geese."
Mark S. Woodrey, "Age-dependent foraging behavior of intercontinental bird migrants during stopover along the northern coast of the Gulf of Mexico."

ROGER TORY PETERSON INSTITUTE TRAVEL AWARD

David S. Pennock, "Seasonal distribution of hatching asynchrony and brood reduction in House Wrens."

ALEXANDER WILSON PRIZE (for best student paper)

Regina Macedo, "Communal breeding behavior in the South American Guira Cuckoo."

SUTTON BIRD ART PRIZE

Rick Fry, "On the Verge."

Selection committee for the Fuertes, Nice, and Stewart Awards—Richard Banks and Richard Stiehl; for the Wilson Prize—Richard Banks, Keith Bildstein, Alfred Dufty, Herb Hendrickson, Judy McIntyre, Pam Rasmussen, and Ernest Willoughby; for the Peterson Travel Award—Jon Barlow, Dick Conner, and Xavier Fazio. Judges for the Sutton Prize—James Dick, John Fitzpatrick, and Robert Storer.

FIRST BUSINESS MEETING

The first business meeting was called to order by President Barlow at 08:38 on Thursday, 16 May in the Forum Room. Secretary Zimmerman summarized the highlights of Wednesday's Council meeting. Next year the Society will meet with the Florida Ornithological Society at the Hilton Inn Gateway West, Kissimmee, Florida from 9–12 April. In 1993 the meeting will be at the University of Guelph, Guelph, Ontario from 29 April to 1 May. The treasurer has reported the Society in excellent shape with income exceeding expenses by about $27,000. The proposed budget for next year totals $102,000. The present membership is 2153 and reflects a 4% decrease from the previous year. Charles Blem has been reelected as editor. A new student travel award, funded by the R. T. Peterson Institute, will be implemented this year. The membership committee under chairperson John Smallwood will be actively soliciting members of the other OSNA societies to join the Wilson Society. Chairperson Keith Bildstein of the Conservation committee requested that he be apprised

of names and organizations that should receive reprints of the committee's report on coastal wetlands that will appear in the June 1991 Bulletin. New business of note is the awarding of a membership in the Wilson Society to students giving papers at annual meetings, including the current meeting. Lastly, Zimmerman asked the membership to stand in honor of members who had died since the last annual meeting—William F. Davis (Kingsville, OH), Guy Greenwell (Neosho, MO), Joseph A. Hagar (Marshfield Hills, MA), Frederic N. Hamerstrom, Jr. (Plainfield, WI), L. Richard Mewaldt (San Jose, CA), Oscar T. Owre (Coral Gables, FL), James T. Tanner (Knoxville, TN), Milton B. Trautman (Columbus, OH), Francis M. Uhler (Bowie, MD).

George A. Hall presented the report of the nominating committee: Richard C. Banks, president; Richard N. Conner, first vice-president; Keith L. Bildstein, second vice-president; Doris J. Watt, treasurer; John L. Zimmerman, secretary; G. Thomas Bancroft for a one-year term as councilor, Robert D. Burns and D. Scott Wood for three-year terms as councilors.

Robert D. Burns gave the treasurer's report.

REPORT OF THE TREASURER
1 January 1990 to 31 December 1990

GENERAL FUNDS

RECEIPTS		
Regular and Sustaining Memberships for 1990	$ 15,265.00	
For 1991	19,223.52	
Student Memberships for 1990	1,879.00	
For 1991	2,117.50	
Family Memberships for 1990	200.00	
For 1991	350.00	
TOTAL DUES		$ 39,035.02
Subscriptions to *The Wilson Bulletin*		
For 1990	$ 19,485.25	
For 1991	2,727.27	
TOTAL SUBSCRIPTIONS		$ 22,212.52
Back Issues of *The Wilson Bulletin*		$ 895.70
Interest and Dividends		$ 31,724.72
Royalties		$ 2,326.72
Contributions from Authors		$ 12,720.00
Contributions to The Van Tyne Library		$ 191.00
Contributions to the Student Membership Endowment		$ 527.00
Contributions to General Endowment (Life Members and Patrons)		$ 1,866.00
Contributions to the Edwards Prize		$ 0.00
Contributions to the Wilson Prize		$ 282.00
Contributions to the General Endowment		$ 213.00
Refund from the 1989 Annual Meeting		$ 1,043.56
TOTAL RECEIPTS		$113,037.24
DISBURSEMENTS: 1990		
The Wilson Bulletin		
December 1989	$ 15,974.61	
March 1990	17,221.30	
June 1990	15,103.22	

September 1990	19,381.56	
Total Printing and Mailing	67,680.69	
Editor's Expenses	3,815.82	
TOTAL PRODUCTION COSTS		$ 71,496.51
OSNA Expenses*		$ 8,573.75
Student Awards		$ 2,600.00
Treasurer's Expenses		$ 192.00
Treasurer's Bond		$ 100.00
Mailings, Student Membership Award Notices		$ 421.99
AAZN Dues		$ 0.00
ICBP Dues		$ 200.00
Subscriptions and OSNA Refunds		$ 0.00
Printing and Mailing of Back Issues		$ 477.35
Incorporation Fee		$ 5.00
Deposit to Endowment		$ 0.00
Meeting Expenses		$ 1,042.40
Van Tyne Library		$ 500.00
TOTAL DISBURSEMENTS		$ 85,609.00

Note: *Newsletter about $3,000.00

BALANCE—Income Less Disbursements ..... $ 27,428.24

CASH ACCOUNTS

Peoples Bank, Gambier, Ohio 43022 31 December 1990		
Checking Account	$ 27,721.11	
Dreyfus Liquid Assets	67,122.35	
TOTAL CASH ON HAND		$ 94,843.46

DESIGNATED ACCOUNTS

LOUIS AGASSIZ FUERTES AND MARGARET M. NICE AWARDS

Endowment Principal		$ 10,000.00
1990 Earnings	$ 700.00	
1989 Balance	$ 500.00	
Award Funds Available	$ 1,200.00	
Funds Disbursed for Awards	$ 700.00	
1990 Cash Balance	$ 500.00	

ALEXANDER WILSON AWARD

Endowment Principal		$ 2,678.41
1990 Earnings	$ 187.49	
1989 Balance	$ (99.10)	
Funds Available	$ 88.39	
Funds Disbursed for Awards	$ 100.00	
1990 Cash Balance	$ (11.61)	

PAUL A. STEWART AWARDS

Endowment Principal		$ 22,649.90
1989 Earnings	$ 1,585.49	
Funds Disbursed for Awards	$ 1,400.00	
1990 Balance	$ 185.49	

George Sutton Color Plate Fund

Endowment Principal		$ 50,000.00
Funds Available Previous Year	$ 4,445.86	
1990 Earnings	$ 3,500.00	
Funds Disbursed for Color Plates	$ 0.00	
1990 Cash Balanee	$ 7,945.86	

Ernest P. Edwards Prize

Endowment Principal		$ 2,456.61
Funds Available	$ 0.00	
Funds Disbursed for Awards	$ 400.00	
1990 Cash Balanee	$ 0.00	
1990 Earnings	$ 160.71	

General Endowment Funds

Endowment Prineipal 1989	$158,222.32
1990 Balanee of General Endowment Prineipal	$162,715.08*

*Based upon $250,500.00 invested at the Mellon Bank

TOTAL ENDOWMENT FUNDS

1989	Amount Invested (Carrying Value)		$250,585.00
	Market Value		$386,992.00
1989	Deposited to Endowment	$ 0.00	
	Endowment Prineipal as of 3-31-91		$250,720.00
	Market Value as of 12-31-90		$372,063.00

Annual Meeting Reserve Funds

1990 Cash Balanee		$ 3,745.76
1990 Meeting Expenses	$1,042.40	
1989 Refund Saint Mary's Meeting	$1,043.56	
Balanee of Centennial Meeting Funds to be Transferred to Student Endowment		$ 3,745.76
1990 Balanee of Meeting Fund		$ 1.16

Robert D. Burns, Treasurer

EDITOR'S REPORT—1990

In 1990, 146 manuseripts (44 major papers, 109 short communieations) were submitted to *The Wilson Bulletin* office. This is 25 fewer than in 1989. Of these, 53% were aeeepted, 42% were rejected, and 5% remain under review. Our aeeeptanee rate over the past several years has been approximately 59% for major papers and 45% for short eommunieations. It is difficult to give exact figures for acceptanee rates. Major papers often are eonverted to short communications before they are published and oecasionally the reverse is true. Papers sometimes are withdrawn before final acceptance (or rejection) has been given. Some authors simply never return revisions of accepted papers. We eurrently are able to give "same day" acknowledgment of reeeipt of new manuscripts and generally aeknowledge revisions within 2–3 days. On the average, we were able to make final decisions about the status of papers

received in 1990 within 60 days. Occasionally, final decision required longer. In all instances this was because of the length of time that referees required to review the manuscript.

I remain grateful to my Editorial Board—Kathy G. Beal, R. N. Conner, C. H. Stinson, and J. R. Walters. They are a constant source of good advice and thoughtful review. George A. Hall continues to edit reviews in a timely, efficient manner. Assistant Editors Leann Blem, Albert E. Conway, and Anne Wenner catch many of the errors that tend to creep into manuscripts. Leann and Robert Blem provide much of the manual labor in running the editorial office. I especially appreciate Kathy G. Beal's efforts in preparing the index for each volume.

We continue to do our best to give rapid response time, quality attention, and personal consideration to each of our potential authors. We appreciate any comments about how to improve the process and encourage ornithologists to call us if they have any questions about how we would handle their work. I enjoy the duties of Editor of *The Wilson Bulletin* and thank the membership for the positive response they have given our performance.

C. R. Blem, *Editor*

The meeting was temporarily adjourned at 08:55 until the second session.

SECOND BUSINESS MEETING

President Barlow opened the second business meeting at 13:30, Saturday, 18 May in the Forum Room. The report of the Auditing Committee was received.

We, the undersigned, have audited the books of the Treasurer, Robert D. Burns, including the ledgers, bank statements and money market statements, and find them in agreement with the Treasurer's report as presented.

We also wish, at this time, to highly commend Dr. Burns for his many years of dedicated service to the Wilson Ornithological Society as Treasurer and thank him on behalf of the Society for his able services.

Doris Watt
Phillips B. Street

It was moved by Dick Banks and seconded by Keith Bildstein to accept this report, and the motion passed.

President Barlow recalled the report of the nominating committee to the floor of the assembly. Additional nominations from the floor were requested, but none were offered. Ken Parkes moved and Phil Street seconded that the nominations be closed and that a unanimous ballot be cast. The motion passed, and a unanimous ballot was duly recorded by the secretary.

REPORT OF THE RESOLUTIONS COMMITTEE

George Hall presented the report of the resolutions committee.

WHEREAS populations of many species of neotropical migrant birds are declining, and

WHEREAS the population status of many other neotropical migrant birds is unknown, and

WHEREAS habitat loss and habitat fragmentation caused by humans in both temperate and tropical environments are major factors in these declines, and

WHEREAS neotropical migrant birds are reflections of the health and condition of both temperate and tropical forests, and

WHEREAS effects of environmental changes on the habitats and populations of migrant birds transcend jurisdictional boundaries, and

WHEREAS there is a pressing need for conservation action and further research on behalf of these birds,

THEREFORE BE IT RESOLVED that the Cooper Ornithological Society and the Wilson Ornithological Society support the coordinated efforts of state and federal agencies, non-governmental organizations, academicians, and international cooperators in the *Neotropical Migratory Bird Conservation Program* to: (1) establish population and habitat monitoring procedures to determine long- and short-term trends, (2) promote conservation efforts for migrant birds across private, public, agency, state, and federal jurisdictional boundaries, (3) promote and coordinate research efforts to provide adequate information for the management of these species, and (4) develop new education, communication, and outreach programs to apprise the public of the status of neotropical migrant birds.

It was moved by George Hall to accept this resolution, seconded by Mary Clench and passed by the membership.

WHEREAS the natural environment of San Clemente Island has been degraded by introductions of feral herbivores and predators, and other anthropogenic factors, and

WHEREAS the habitat of the San Clemente Loggerhead Shrike (*Lanius ludovicianus mearnsi*) and those of other native species have been severely degraded by feral pigs and goats, and

WHEREAS populations of many native vertebrates are vulnerable to predation by common ravens, rats, and feral cats, and

WHEREAS recovery of the shrike population in its natural environment as presently constituted appears unlikely,

THEREFORE BE IT RESOLVED that the Cooper Ornithological Society and the Wilson Ornithological Society urge the United States Fish and Wildlife Service and the California Department of Fish and Game to support fully the captive breeding and habitat restoration efforts recently undertaken by the Department of Defense, United State Navy; the Zoological Society of San Diego; the University of California, Berkeley; the University of California, Riverside; and the Western Foundation of Vertebrate Zoology.

AND FURTHERMORE BE IT RESOLVED the Cooper Ornithological Society and the Wilson Ornithological Society urge the United States Fish and Wildlife Service and the California Department of Fish and Game to initiate a program of habitat restoration with goals of providing suitable conditions for the conservation of all native flora and fauna of the island, and returning the San Clemente Loggerhead Shrike to its native environment as quickly as possible.

It was moved by George Hall and seconded by Clait Braun to accept this resolution and the motion passed.

WHEREAS long-term studies are essential for understanding mechanisms that influence population dynamics of vertebrates, especially long-lived species such as the California Gull (*Larus californicus*), and

WHEREAS the 33-year-old population study of California Gulls at Bamforth Lake, Wyoming, is the second largest active population study of birds in North America,

THEREFORE BE IT RESOLVED that the Cooper Ornithological Society and the Wilson Ornithological Society commend past and continuing support provided by the Wyoming Game and Fish Department in ensuring that this very important population study can and will continue.

It was moved by George Hall and seconded by Elden Martin to accept this resolution, and the membership voted in favor.

WHEREAS the California Gnatcatcher (*Polioptila californica*) apparently has been eliminated from the California counties of Ventura and San Bernardino, and

WHEREAS the species' once extensive distribution in Los Angeles County has been reduced to a small portion of the Palos Verdes Peninsula, and

WHEREAS the California Gnatcatcher recently has been recognized as taxonomically distinct from the Black-tailed Gnatcatcher (*P. melanura*), and

WHEREAS the species is an obligate, permanent resident of coastal sage scrub, a unique and diverse vegetation type that many consider to be one of the most endangered habitats in the continental United States, and

WHEREAS intense housing development and expansion of transportation corridors in Orange, Riverside, and San Diego counties threaten to eliminate the few remaining large tracts of California Gnatcatcher habitat within the next 20 years, and

WHEREAS the impact of such habitat loss will compound the effects of extensive habitat fragmentation, and

WHEREAS estimates of the numbers of individuals of this species presently occurring in the United States range from 1200 to 2000 pairs, and

WHEREAS conservation and mitigation efforts required by existing regulatory mechanisms have, in general, failed to protect adequately viable populations of the species, and

WHEREAS without full protection under the Federal Endangered Species Act and prompt development of an effective regional recovery plan, there is overwhelming evidence that populations of this species will continue to decline, and that the species will be extirpated from all or most of its range in the United States,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society and the Cooper Ornithological Society recommend that the United State Fish and Wildlife Service immediately undertake emergency listing of this species under the provisions of the Federal Endangered Species Act, and that the Service establish a recovery plan to ensure the protection of this species and its habitat.

It was moved by George Hall, seconded by Dick Hunter, and passed by the members present to accept this resolution.

WHEREAS the use of large-scale driftnets is an indiscriminate and destructive method of fishing that kills seabirds and other living marine resources in the world's oceans, and

WHEREAS there may be severe adverse impacts of high-sea driftnets on seabirds and other marine resources as preliminary estimates indicate that at least 875,000 seabirds die annually in North Pacific driftnets alone, and

WHEREAS jurisdiction over seabirds under the United States Migratory Bird Act extends only three miles from the coast of the United States, whereas the United States protects marine mammals from driftnets and other threats out to 200 miles,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society and Cooper Ornithological Society support banning large-scale, high-seas driftnets in the world's oceans as stated in United National Resolution 44-225, United States Public Law 101-627, and the Wellington Convention, and

FURTHERMORE BE IT RESOLVED that the Wilson Ornithological Society and Cooper Ornithological Society urge the United States Congress to amend the Migratory Bird Treaty Act to extend jurisdiction of the United States over migratory birds to 200 miles off of its coasts.

It was moved by George Hall and seconded by Judy McIntyre to accept this resolution. The motion passed.

WHEREAS the Cooper Ornithological Society held its Sixty-first Annual Meeting and the Wilson Ornithological Society held its Seventy-second Annual Meeting jointly in Norman, Oklahoma, on the campus of the University of Oklahoma at the invitation of the Department of Zoology, Oklahoma Biological Survey, and Oklahoma Museum of Natural History (all of the University of Oklahoma), the Cleveland County Audubon Society, and the Oklahoma Ornithological Society, and

Recognizing that the Committee on Local Arrangements, under the outstanding direction

of Gary D. Schnell, provided us with an exceptionally diverse assemblage of exhibits, speeial events, field trips, and evening social events, and

Recognizing that the Committee on the Seientifie Program, under the equally eapable direction of Richard N. Conner, arranged outstanding seientific leeture sessions, workshops, and poster sessions, and

WHEREAS all those who have attended this meeting have been enriehed by it,

THEREFORE BE IT RESOLVED that the Cooper Ornithologieal Soeiety and the Wilson Ornithological Soeiety commend the Committee on Loeal Arrangements and the Committee on the Seientific Program for their efforts towards this memorable meeting, and

THEREFORE BE IT FURTHER RESOLVED that the Cooper Ornithologieal Society and the Wilson Ornithologieal Soeiety also thank other supporters of this meeting, namely, the Offiee of Research Administration (University of Oklahoma), University of Oklahoma Foundation, Oklahoma City Zoo, University of Oklahoma Press, University of Texas Press, Fuhrman Diversified, Ine., and an anonymous donor for their most generous support.

It was moved by George Hall and seeonded by Kenneth Parkes to aeeept this resolution, and it was unanimously aeeepted.

WHEREAS Robert D. Burns has served the Wilson Ornithologieal Society long and well as its treasurer, and

WHEREAS the Soeiety has reaped the many benefits of his assiduous reestablishment of its finaneial integrity and his eareful (even eanny) husbandry of its assets, a time-eonsuming and sometimes underappreeiated task, and

WHEREAS Bob is now retiring after 12 years of serviee to the Society and has trained his suceessor to ensure equally eareful handling of its finances in the future,

THEREFORE BE IT RESOLVED that the Offieers, Couneil, and Membership of the Wilson Ornithologieal Soeiety express their sineere gratitude to Bob Burns for a job well done!

It was moved by George Hall to aeeept this resolution, seeonded by aeelamation and passed by a standing ovation.

It was moved by Mary Cleneh and seeonded by Diek Banks that the meeting be adjourned, and it was.

The reports of the standing eommittees are as follows.

REPORT OF JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE—1990

The ealendar year 1990 was another aetive and sueeessful one for the library. The facilities in the Univ. Miehigan Bird Division have been improved, and eontinuing adjustments made, all of whieh help to make our operations more effeetive. The figures to follow indieate that mueh has been going on. The real responsibilities for this eontinue to rest on the always-eapable (if overburdened) shoulders of Janet Hinshaw. The ehairman owes to her never-ending expression of gratitude; and the whole membership should be kept aware of her serviees.

That our members continue to consider the library worthy of their support is demonstrated by the total of 493 items, plus funds, donated by 21 members. Reeeived were 263 journal issues, 12 books, 97 monographs and reports, and 121 reprints and pamphlets. Notable contributors were A. J. Berger, P. Baird, W. Bowlen, R. C. Banks, C. Collins, G. A. Hall, J. Hinshaw, S. Houston, S. Holohan, L. J. Harris, F. Hammerstrom, D. Koenig, H. Mayfield, M. K. Nicholl, H. Mueller, R. B. Payne, J. Priee, W. J. Richardson, G. Filteau (for La Societe Zoologique de Quebee), P. Stettenheim, and H. Zerniekow.

Donations, if not items that can go direetly onto our shelves, are nevertheless disposed of profitably. Two books sold in 1990 brought in $20; within the next few years a number

are expected to be sold from our large stock of duplicates. We also hope for a continuing brisk turnover of separates. Our New Book Fund now receives an additional annual sum of $500. From this fund, direct purchases were made of 5 books, 6 monographs, 2 dissertations, and 19 journal volumes, for $512.15. Subscriptions ($344.20) paid for 9 journal volumes.

Exchanges with 124 other institutions provided us a total of 162 journal titles. Gifts from 38 institutions and individuals added 44 more. By 12 direct subscriptions, were added 16 titles, making a grand total of 222 journals from 174 institutions, organizations, and members.

On the other side of the coin, the Josselyn Van Tyne Memorial Library has continued to supply to the Society membership and others the kind of invaluable services of which it is capable. During 1990, 42 members and libraries borrowed 317 items in 64 transactions. This does not take into account the continuous in-house reference to items on our shelves.

A plea for even more membership support, both in contributions and in personal use, is always in order. Remember too, that numerous publications of all sorts are on sale, at fair prices, from our large stock of duplicates.

William A. Lunk, *Chair*

REPORT OF THE CONSERVATION COMMITTEE

The committee's report, entitled "Approaches to the conservation of coastal wetlands in the Western Hemisphere," will appear as a 38-page paper in the June 1991 issue of The the Western Hemisphere," will appear as a 38-page paper in the June 1991 issue of *The Wilson Bulletin.* Council has authorized the purchase of 200 reprints of this report, which hemisphere. If you know of anyone who should receive a copy of this report, please let me know.

The committee is currently working with W. M. Block, who chairs the COS Committee of Conservation and Resolutions, on several joint resolutions to be acted upon at the Oklahoma meeting.

If anyone has any conservation issues they feel WOS should explore, please let me know, and I will see what I can do.

Keith L. Bildstein, *Chair*

REPORT OF THE MEMBERSHIP COMMITTEE

The updated membership brochure is now available. A total of 5000 were printed; I'll be happy to send (large numbers of) brochures to WOS members who request them! A supply of brochures has already been sent to a few members and to Allen Press.

I have obtained from Allen Press 2817 mailing labels for all OSNA members who are not members of the WOS. During the next few months the membership committee plans to send a brochure and letter of invitation to join our society to each of these people.

Greg Butcher, AFO membership chair, has begun a campaign aimed at increasing the number of lucrative institutional subscriptions to the four OSNA journals. In the near future, each OSNA member will receive a mailing urging them to visit their institution's procurement librarian in person to stress the importance of new or continued subscription to these journals. The mailings will be the results of Greg's efforts, and will be funded by the four societies.

For the committee (Jim Ingold, Mark Woodrey, Tom Waite, and Ken Meyer),

John A. Smallwood, *Chair*

The Committee on Scientific Program was chaired by Richard Conner and facilitated by the following session moderators: Richard C. Banks, Mary H. Clench, Mercedes S. Foster, Joseph A. Gryzbowski, Jerome A. Jackson, John T. Rotenberry, Stephen M. Russell, James A. Sedgwick, Charles R. Smith, Deborah M. Smith, Kimberly G. Smith, Diana F. Tomback, Doris J. Watt, John L. Zimmerman.

PAPER SESSIONS

William S. Clark, Alexandria, VA, and Richard C. Banks, U.S. Fish & Wildl. Serv., Natl. Mus. Nat. Hist., Washington, DC. "Taxonomic status of the White-tailed Kite."

Mary H. Clench, Div. Gastroenterology, Dept. Internal Med., Univ. Texas Medical Branch, Galveston, TX. "The systematic position of MacGregor's Bird-of-Paradise: a ptcrylographic contribution to the problem."

William H. Baltosser, Dept. Biol., Univ. Arkansas, Little Rock, AR. "Geographic variation in the Black-chinned Hummingbird (*Archilochus alexandri*)."

Raymond Pierotti, Dept. Biol. Sci., Univ. Arkansas, Fayetteville, AR. "Phenotypic plasticity, Lack's paradox, and 'cost-free' reproduction: why means are of little meaning in population biology."

John M. Bates, Mus. Nat. Sci., & Dept. Zool. & Physiol., Louisiana State Univ., Baton Rouge, LA. "Evolutionary relationships in the tyrannid genus *Leptopogon,* with comments on the evolution of Andean birds."

Pamela C. Rasmussen and Phillip S. Humphrey, Mus. Nat. Hist., Univ. Kansas, Lawrence, KS. "A postglacial record of the avifauna of the Beagle Channel from Indian middens."

Robert W. Storer, Mus. Zool., Univ. Michigan, Ann Arbor, MI. "The occurrence and possible significance of ossified tendons in Western and Clark's grebes."

Brian A. Maurer and S. Grey Heywood, Dept. Zool., Brigham Young Univ., Provo, UT. "Measuring geographic range fragmentation in passerine birds."

Charles van Riper III, Natl. Park Serv., Coop. Park Stud. Unit, Northern Arizona Univ., Flagstaff, AZ, Susan L. Skiff, Dept. Wildl. & Fish. Biol., Univ. California, Davis, CA, and Jan van Wagtendonk, Yosemite Natl. Park, Yosemite Natl. Park, CA. "Integration of a backcountry survey and geographic information system for Great Gray Owls in Yosemite National Park."

Sally Graves Jackson, Dept. Fish. & Wildl., Utah State Univ., Logan, UT. "Birds in willow stands in and around northern Yellowstone National Park: how do native ungulates affect these assemblages?"

Jeffrey David Parrish and Thomas W. Sherry, Dept. Ecol., Evol. & Organismal Biol., Tulane Univ., New Orleans, LA. "Sexual habitat segregation in American Redstarts wintering in Jamaica."

Martin L. Morton, Occidental Coll., Los Angeles, CA. "Postfledging dispersal of Green-tailed Towhees to a subalpine meadow."

K. C. Jensen, Dept. Wildl. & Fish. Sci., Texas A&M Univ., College Station, TX. "Habitat selection by molting Pacific Black Brant in Alaska."

Holly Edwards, Dept. Zool., Univ. Oklahoma, Norman, OK. "Natural remanent magnetization in birds."

Laura L. Erickson and Kim R. Eckert, Duluth, MN. "Daytime warbler migration in fall along Lake Superior's north shore."

Michael F. Carter, Colorado Bird Observatory, Brighton, CO. "Regional population trend data sets——an example from Colorado."

Kenneth L. Petersen, Dept. Biol., Monmouth Coll., Monmouth, IL, and Louis B. Best, Dept. Animal Ecol., Iowa State Univ., Ames, IA. "Mapping bird territories using the flush technique: the potential for bias and misinterpretation."

R. Kannan, Dept. Biol. Sci., Univ. Arkansas, Fayetteville, AR, and David T. Kee, Dept. Biol., Northeast Louisiana Univ., Monroe, LA. "Do northbound migratory passerines have more pesticide residues than southbound forms?"

Stephen M. Russell and Ruth O. Russell, Dept. Ecol. & Evol. Biol., Univ. Arizona, Tucson, AZ. "Autumnal 'wintering' of Anna's Hummingbird in Arizona."

Frank F. Rivera-Milan, Dept. Nat. Res., Sci. Res. Area, Terrestrial Ecol. Sec., Pta. de Tierra, PR. "Distribution and relative abundance of columbids in Puerto Rico."

Steven R. Sheffield and William L. McClure, Dept. Zool., Oklahoma State Univ., Stillwater, OK. "The effects of living on a hazardous chemical waste site on a family of Barn Owls (*Tyto alba*)."

John L. Zimmerman, Dept. Biol., Kansas State Univ., Manhattan, KS. "Density-independent factors and prairie bird populations."

Eileen M. Kirsch, Dept. Biol., Sci., Univ. Montana, Missoula, MT. "Productivity and the importance of chick survival in Least Terns on the lower Platte River, Nebraska."

Kevin Winker, Bell Mus. Nat. Hist., Univ. Minnesota, Minneapolis, MN, John H. Rappole, Cons. & Res. Center, Natl. Zool. Park, Front Royal, VA, and Mario A. Ramos, World Wildl. Fund U.S., Washington, DC. "The nonbreeding territory: food resource or shelter from predation?"

Donald R. Powers, Dept. Biol., George Fox Coll., Newberg, OR. "Hummingbirds: a review of metabolic rate data."

David L. Swanson, Dept. Biol., Univ. South Dakota, Vermillion, SD. "Seasonal and growth hormone effects on substrate metabolism under cold stress in Dark-eyed Juncos."

Alfred M. Dufty, Jr., Dept. Biol., Boise State Univ., Boise, ID. "Songs and calls in a free-living bird: seasonal patterns and their relationship to circulating testosterone levels."

Michael D. Bay, Dept. Biol. Sci., Univ. Arkansas, Fayetteville, AR. "Structure and geographic variation in the type B song of the Northern Parula."

Michael T. Green, Dept. Biol., Univ. North Carolina, Chapel Hill, NC. "Song variability in Baird's Sparrows."

Greg H. Farley, Dept. Biol., Univ. New Mexico, Albuquerque, NM. "The energetics of roosting behavior in *Campylorhynchus* wrens."

Lisa M. Ellis, Dept. Biol., Univ. New Mexico, Albuquerque, NM. "Female subadult plumage: support for the molt-constraints hypothesis for delayed plumage maturation in North American passerines."

Thomas C. Michot and Paul C. Chadwick, U.S. Fish & Wildl. Serv., Louisiana State Univ., Baton Rouge, LA. "Lipid mass of Louisiana Redheads increases through winter."

Marc C. Woodin, U.S. Fish & Wildl. Serv., Corpus Christi, TX, and Patrick L. Parker, Univ. Texas, Marine Sci. Inst., Port Aransas, TX. "Variation of ratios of stable carbon isotopes in wintering and breeding Redheads."

Douglas A. James, Dept. Biol. Sci., Univ. Arkansas, Fayetteville, AR. "Identifying hummingbirds using indirect measurements."

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John W. Fitzpatrick, Archbold Biol. Sta., Lake Placid, FL. "The program of Conservation International."

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Joseph A. Grzybowski, Dept. Zool., Univ. Texas, Austin, TX. "Black-capped Vireos, cowbirds and habitat deterioration."

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Bret W. Tobalske, Dept. Biol. Sci., Univ. Montana, Missoula, MT. "Evaluating habitat suitability through measures of reproductive success and feeding behavior in Red-naped Sapsuckers."

Richard N. Conner and D. Craig Rudolph, Southern For. Experiment Sta., Nacogdoches, TX. "The rise and fall of the southern pine ecosystem and Red-cockaded Woodpecker."

Barbara Raulston, Dept. Biol. Sci., Arkansas Coop. Fish & Wildl. Res. Unit, Univ. Arkansas, Fayetteville, AR. "Use of restricted cavities by Red-cockaded Woodpeckers."

D. Craig Rudolph and Richard N. Conner, Southern For. Experiment Sta., Nacogdoches, TX. "History of, and recent advances in augmentation and reintroduction techniques for Red-cockaded Woodpeckers (*Picoides borealis*)."

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Dodge Nature Center, St. Paul, MN. "Female-skewed sex ratios in late nests of Eastern Bluebirds in northwestern Arkansas."

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Leonard A. Brennan, Dept. Wildl. & Fish., Mississippi State Univ., Mississippi State, MS and Michael L. Morrison, Dept. For. & Resource Mgmt., Univ. California, Berkeley, CA. "Time-series analyses of avian foraging behavior."

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David S. Pennock, Dept. Biol. Sci., Univ. Arkansas, Fayetteville, AR. "Seasonal distribution of hatching asynchrony and brood reduction in House Wrens."

Doris J. Watt, Dept. Biol., St. Mary's Coll., Notre Dame, IN. "Environmental influence on hatching asynchrony in the American Goldfinch."

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Neil Buckley, Dept. Zool. & Oklahoma Biol. Surv., Univ. Oklahoma, Norman, OK. "Communal roosting and the role of information transfer in the foraging behavior of Turkey Vultures and Black Vultures."

Charles R. Paine, Coop. Wildl. Res. Lab. & Dept. Zool., Southern Illinois Univ., Carbondale, IL and Thomas C. Tacha, Caesar Kleberg Wildl. Res. Inst., Texas A&I Univ., Kingsville, TX. "The importance of biparental care in Canada Geese during brood rearing."

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Douglas W. Mock and Timothy C. Lamey, Dept. Zool., Univ. Oklahoma, Norman, OK. "How egret nestlings negotiate a ceasefire."

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James L. Ingold, Dept. Biol. Sci., Louisiana State Univ., Shreveport, LA and Vincent LaPolla, Dept. Zool., Miami Univ., Oxford, OH. "Intraspecific variation in the distress calls of the Northern Cardinal and Gray Catbird."

John C. Kricher, Dept. Biol., Wheaton Coll., Norton, MA, and William E. Davis, Jr., Dept. Sci. & Math, Coll. Basic Stud., Boston Univ., Boston, MA. "Species richness patterns and site fidelity among resident birds in disturbed and undisturbed moist forest in southern Belize."

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Janet R. Mihuc and Charles H. Trost, Dept. Biol. Sci., Idaho State Univ., Pocatello, ID. "Probing shorebird predation on invertebrates at an inland site."

Darrell W. Pogue, Dept. Zool. & Oklahoma Biol. Surv., Univ. Oklahoma, Norman, OK. "Nesting-habitat ordination of secondary cavity-nesting birds in Oklahoma."

John T. Rotenberry, Nat. Reserve System, Univ. California, Riverside, CA. "Dynamics of patch selection by foraging shrubsteppe sparrows."

Patricia L. Schwagmeyer, Douglas W. Mock, Timothy C. Lamey, and Camelia S. Lamey, Dept. Zool., Univ. Oklahoma, Norman, OK, and M. D. Beecher, Dept. Psychol., Univ. Washington, Seattle, WA. "Talking eggs: sibling contact effects on hatch timing in an asynchronously hatching gull."

Ernest J. Willoughby and Marie Cox, Dept. Nat. Sci. & Math., St. Mary's Coll. Maryland, St. Mary's City, MD. "Vocal repertoire of the Chipping Sparrow."

Steve Labuda and Mike Morrow, Attwater Prairie Chicken Natl. Wildl. Refuge, Eagle Lake, TX, and Douglas Jost, Lisl Shoda, Martin Whiting and K. C. Jensen, Dept. Wildl. & Fish. Sci., Texas A&M Univ., College Station, TX. "A hierarchical recovery plan for the Attwater's Prairie-Chicken."

Angela A. Fangmeier, Dept. Zool., Univ. Oklahoma, Norman, OK. "Begging and feeding behavior in the Cattle Egret (*Bubulcus ibis*)."

ATTENDANCE

ARIZONA: *Flagstaff,* Charles Van Riper III, Paul E. Super; *Tempe,* William M. Block, Glenn Walsberg; *Tucson,* Tom Huels, Ruth Russell, Steve Russell.

ARKANSAS: *Fayetteville,* Charles Amlaner, Jr., Miguel Armella, David Barber, Michael D. Bay, Susan L. Bay, Robert Doster, Douglas James, Ragupathy Kannan, David S. Pennock, Jack Mobley, Patti Moore, Ray Picrotti, Barbara Raulston, Mia Revels, Kimberly Smith, Dora Weyer; *Little Rock,* William H. Baltosser.

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VERMONT: *Burlington,* Jay J. Rotella.
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WEST VIRGINIA: *Morgantown,* George A. Hall.
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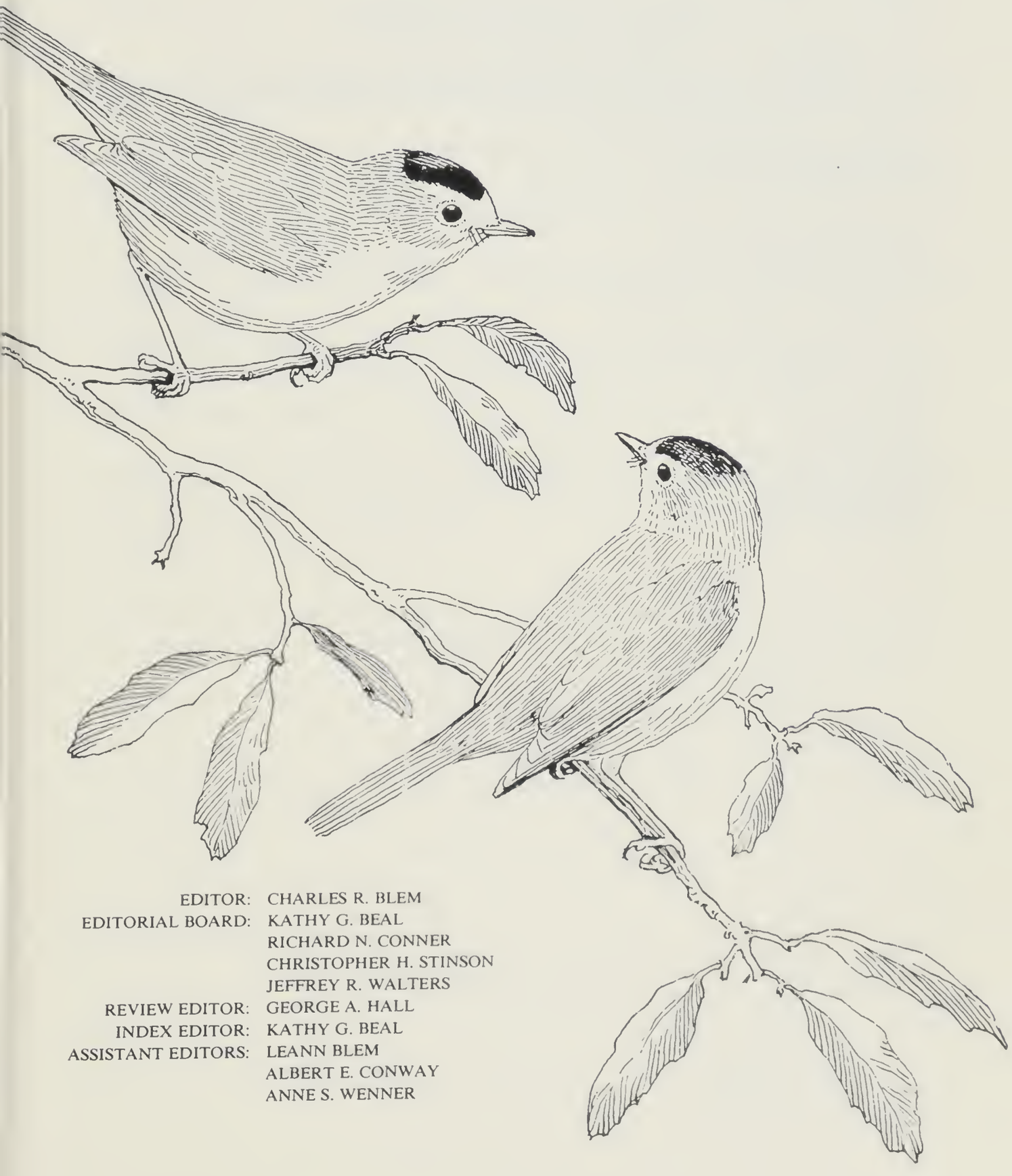

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